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Recent Developments in Neuroscience Research on Human Motivation

Sung-il Kim
Johnmarshall Reeve
Mimi Bong
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RECENT DEVELOPMENTS IN NEUROSCIENCE RESEARCH ON HUMAN MOTIVATION

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INTRODUCTION TO MOTIVATIONAL NEUROSCIENCE

Sung-il Kim, Johnmarshall Reeve and Mimi Bong

ABSTRACT

The rapid progress of neuroscience and the interdisciplinary collaboration between neuroscience and psychology have begun to provide valuable insights for understanding the dynamic and implicit nature of human motivation by identifying the in vivo neural mechanism of motivation. One of the fundamental questions in the field of the neuroscience of motivation is what neural mechanisms underlie the direction, intensity, and guidance of our motivation and subsequent actions. This prologue explains how neuroscience can contribute to the understanding of human motivation. To accomplish this purpose, we present what neuroscientific data look like, identify 13 key motivation-relevant brain structures, and introduce 3 key motivation-centric brain circuits – namely, the reward circuit, the value-based decision-making pathway, and the self-regulation/self-control network.

Keywords: Motivation; neuroscience; reward circuit; value-based decision-making; goal-directed control

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INTRODUCTION

With the recent advent of cognitive, social, affective, and developmental neuroscience, psychological constructs and theories in all domains of psychology have undergone fundamental reconceptualization. The reason why neuroscience has been so instrumental in rethinking all fields in psychology is because it provides new insights, new knowledge, and new perspectives that have enriched – and even renewed – each domain it touches.

What can motivation study learn from a new focus on neuroscience? An important question in understanding the link between the brain and motivation is how the brain directs and energizes behavior. Specifically, what are the neural mechanisms that underlie the selection, intensity, and persistence of an action among competing alternatives? By focusing on neuroscientific investigations regarding these important questions, we present an overview of what is currently understood about the neural basis of motivation.

This prologue begins by briefly introducing the contribution neuroscience can make to understanding human motivation. It then introduces the reader to what neuroscientific data look like and how they are best interpreted and used. The chapter identifies 13 motivation-relevant brain structures as well as 3 key motivation-centric brain circuits. By following this structure, this prologue chapter is meant to position the reader to better appreciate and understand the 12 chapters on motivational neuroscience that follow.

WHY NEUROSCIENCE?

Current theories of motivation are limited by three significant shortcomings (Kim, 2013). The first is the conceptual vagueness and overlap among many motivation-related constructs. For instance, the distinctions between intrinsic motivation and interest, self-efficacy and competence, and self-regulation and volition are not clear. If these motivational constructs are unique components of different theories, then the underlying mechanisms of each construct should also be different. This is a problem in contemporary motivation theory because the number of motivation theories seems to proliferate without any built-in constraints (Hulleman, Schrager, Bodmann, & Harackiewicz, 2010).

For example, the motivational concepts of self-efficacy, ability beliefs, and the need for competence are all considered distinct constructs by different motivation theorists. A neuroscientist would activate each of these four motivational states (e.g., by presenting exposure to a coping model, success feedback, or optimal challenge, respectively) and see if four distinct patterns of neural activity could be observed. If not, then it seems a fair question to ask how distinct these four motivational constructs really are. On the other hand, if four distinct patterns of neural activity were observed, then that would support the idea that these are indeed four distinct constructs.

Second, no adequate definition of motivation yet seems to exist. For instance, the classic definition of "any process that energizes and directs behavior" merely identifies what motivation does (i.e., energizes and directs behavior) without really identifying what motivation itself actually is. Given the ambiguous definition of motivation, existing theories focus only on partial aspects of motivation. Reinforcement theory is concerned with overt behavioral changes whereas self-determination theory emphasizes internal needs. Goal theory emphasizes cognitive representations of future outcomes, whereas attribution theory emphasizes cognitive representations of past experiences. Current theories of motivation tend to identify the various sources of human satisfaction but not being able to adequately answer the following more fundamental questions: How are experiences such as want, desire, and satisfaction created? How do individuals anticipate satisfaction? How do individuals select a particular action among several competing alternatives? Why do individuals persist in an action even if they do not expect feelings of satisfaction? How does motivation develop over time?

From a wider perspective, motivation theories fall short of fully accounting for the dynamic mechanisms of human motivational processes. This is probably because motivation is a multifaceted phenomenon which has diverse sub-processes. The quality of motivation, which changes over time, differs depending on the stage of the motivational process. For example, the mechanism by which initial motivation is triggered (e.g., a challenge to strive for) might be qualitatively different from the mechanism by which motivation is maintained and regulated, such as the enhanced "sense of agency" arising from the integration of values and goals. To understand the dynamic nature of human motivation, variations in motivational state should be consistently examined through the lens of a grand theory, rather than separate theories based on individual motivation-related phenomena (Baumeister, 2016).

Third, most measures of motivation are derived from subjective self-reports from participants regarding their internal state. These reports rely heavily on the overall estimation of past experiences or attitudes, which cannot be easily observed or verified by a third person. Our introspective capacity is quite limited (Wilson & Dunn, 2004) and human motivation is not always conscious and deliberate. Rather it is more likely to be unconscious, implicit, and automatic (Dijksterhuis & Aarts, 2010).

Although it is possible to study motivation via surveys or field experiments, self-report surveys and behavioral observations are limited in capturing the exact cognitive and affective processes that are taking place in conjunction with motivation processes because people have only restricted conscious access to their own emotions and cognitions (e.g., Panksepp, 2005). Survey research is thus fundamentally restricted in its ability to reveal the ongoing generation, maintenance, and regulation of motivation or to grasp the qualitative differences between various motivational states. In addition, because participants may not be aware of or want to reveal their motivation and emotion, the use of self-reports is constrained to consciously accessible and socially desirable aspects of motivation. This is why a science requires objective measures, or at least the blending of objective and subjective measures.

These serious limitations can be overcome by measuring the neural underpinnings of implicit cognitive and affective processes using brain imaging techniques, which allow for the identification of in vivo motivational processes. In the motivational neuroscience approach, neuroimaging techniques are combined with experimental and survey methods to gain a better insight into motivational phenomena that behavioral or self-report measures alone may not provide. By analyzing brain regions that show differential activation, concerns about social desirability, false or selective recollection, and insincere or otherwise unreliable responses can be avoided. In addition to helping overcome the limitations of subjective (self-report) measures, neuroscientific data adds new, objective measures of motivation.

Caveat

When we interpret results from neuroimaging studies, there are several considerations to be kept in mind. Here we identify four key concerns in using neuroscientific data to advance motivation study.

First, brain imaging data is basically correlation between a task and brain activity. That is, when participants engage in a task or receive some sort of stimulus, they show simultaneous brain activations. These correlated neural activities do not provide direct information about causality, because it cannot be determined whether the brain activity caused the motivational state or the motivational state caused the brain activity.

Second, when the cognitive and affective states are inferred from neural activation, the so-called "reverse inference" problem can arise. Because individual brain regions are not exclusively involved in a single process, we need to be cautious when drawing conclusions about mental processes on the basis of observed neural activities in any given regions of the brain. Of course, converging evidence on functional neuroanatomy or functional connectivity of the brain network can decrease the probability of generating a reverse inference.

Third, experimental tasks and materials are inherently limited. A typical experimental task needs to be rather simple, such as pressing a button when a correct answer appears but pressing a different button when an incorrect answer appears. The timescale used in neuroscience experiments is also very limited – just a few seconds. So the data collected are often the records of brain activations and their reaction times. This is very different from psychological studies of motivation, obviously, which might study how beliefs are developed over the course of a semester or how the quality of the teacher-student relationship might change week-to-week.

Fourth, the temporal and spatial resolution of even the cutting-edge technology is still limited. Fortunately, recent advances in statistics and brain imaging technology (e.g., diffusion tensor imaging, DTI; repetitive transcranial magnetic stimulation, rTMS) suggest that these limitations are becoming less of a concern with each passing day.

NEUROSCIENTIFIC DATA

As mentioned earlier, contemporary motivation studies in educational contexts routinely measure motivational states with self-report questionnaires, interview protocols, behavioral measures such as effort and choice, and ratings made by teachers, peers, or classroom observers. These are all valid ways to assess motivation. Neuroscientific data, however, are different. Neuroscientific data are various measures of brain activity, and the two methods to measure brain activity that appear most frequently in the following chapters are functional magnetic resonance imaging (*f*MRI) and electroencephalogram (EEG) event-related potentials.

Fig. 1 shows both the equipment used to collect these data (a and b) and what the collected data look like (c and d). During *f*MRI assessment, as Fig. 1a shows, participants lay on a bed and slide into a large machine that uses magnets to record the structure of the person's brain (MRI) as well as changes in the brain fuel (glucose) that occurs when various parts of the brain function or are used (*f*MRI). Consumption of glucose is a marker of brain activity, and this is what *f*MRI monitors. As shown in Fig. 1c, these brain activations show up on a brain scan as changes in activity in different regions of the brain. In the *f*MRI brain scan shown, the participant showed increased activity in the anterior insula while being engaged in an optimally challenging (i.e., interesting) task.

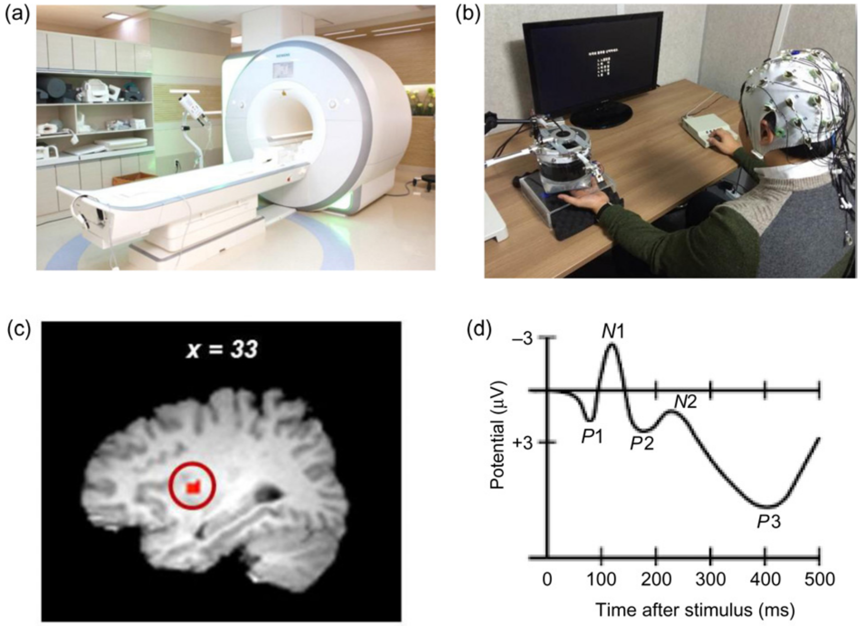

Fig. 1. The left half shows an *f*MRI scanner (a) and the data (c). The right half shows an EEG cap (b) and the data (d).

During EEG assessment, as Fig. 1b shows, participants wear a cap that has anywhere from 10 to 256 (often 20) sensors to record signals from the brain activity, monitored by these sensors while the participant completes some experimental task (e.g., reading text displayed on a computer screen). As shown in Fig. 1d, EEG brain signals are monitored as waveforms to communicate the rise and fall (activation and de-activation) of the brain signals from different parts of the brain. EEG data reflects event-related brain potentials (ERPs), in which the "event" is an external (picture) or internal (memory) stimulus. The EEG waveform typically reflects five post-stimulus brain events: *P*1; *P*2; *P*3; *N*1; and *N*2. These five terms are named for their polarity (*P* = positive; *N* = negative) and for their ordinal position after the stimulus onset (1 = 100 ms; 2 = 200 ms; 250 = 250 ms; 400 = 400 ms). Brain activity occurring 100-250 ms after the stimulus onset generally reflects sensory processing (vision, audition), while brain activity occurring 250 ms and more after the stimulus onset generally reflects cognitive processing (appraisal, interpretation). For example, a spike at N250 often signals that the person experienced a cognitive miss-match against what they expected to happen. The N250 spike reflects the recruitment of executive cognitive control to resolve the experienced discrepancy.

THIRTEEN CORE BRAIN STRUCTURES

*f*MRI and EEG equipments measure the activity of specific brain structures. Here we introduce 13 brain structures that are frequently observed during neuroscientific motivation studies, such as those that will be reviewed in the chapters that make up this volume. Here we simply introduce these 13 brain structures, provide their commonly used abbreviations, briefly state their motivational functions, and identify their anatomical locations, as shown in Fig. 2. In introducing the motivational functions associated with each brain structure, we must remind the readers again that any individual brain structure is associated with many different brain functions – including those that are not motivational in nature – that are not mentioned below (e.g., the dorsolateral prefrontal cortex is involved in the emotion regulation but it is better known for its key role in working memory or human intelligence). In addition, it is important to note that all of these brain structures have bilateral representation in the brain (the structure is present on both the right and left sides of the brain).

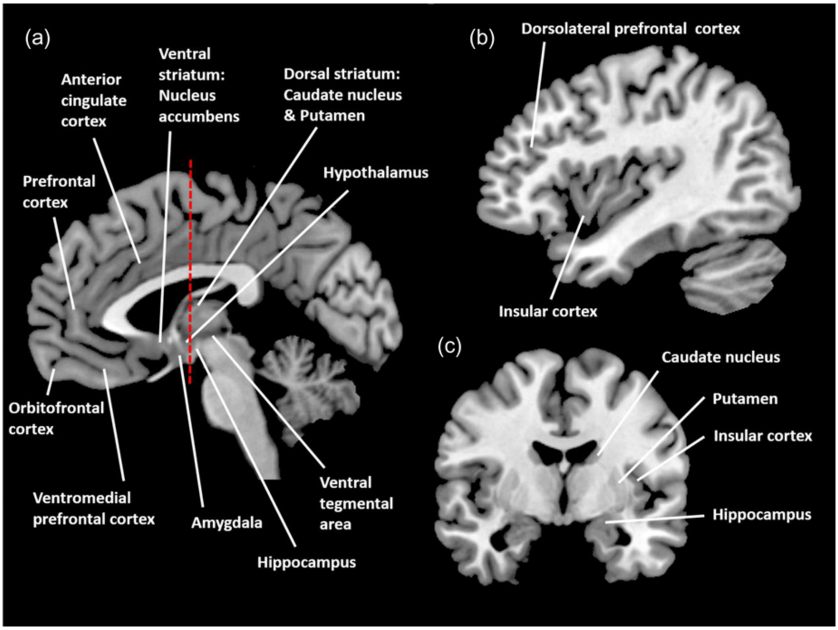

Fig. 2. Anatomy of 13 key motivation-relevant brain structures. A medial sagittal (a), a lateral sagittal (b), and a coronal (c) sections of the human brain.

Five cortical brain structures are highly relevant to motivational states. The prefrontal cortex (PFC) lies behind the forehead and is most notable as the neural home of conscious, deliberate goals as well as of cognitive interpretations and appraisals. The orbitiofrontal cortex (OFC) lies under the PFC, and is the brain structure that processes and stores value-related information about environmental objects (which can be used to form preferences and to make choices). The ventromedial prefrontal cortex (vmPFC) processes and stores affect-based information associated with sensory and social stimuli. The dorsolateral prefrontal cortex (DLPFC) retains goals and involves in cognitive control. The anterior cingulate cortex (ACC) monitors conflict in information processing and, when conflicts arise, recruits increased allocation of cognitive resources (e.g., attention, decision-making) from other cortical brain structures to resolve the conflict.

Two brain structures are anatomically located in between the cortical and subcortical brain. The hippocampus (a Latin word for its "seahorse" shape) is involved in the storage of long-term memory information, especially declarative information such as facts or events. The anterior insular cortex (AIC), or simply "insula," lies deep within the brain and is part cortical and part subcortical. The insula receives, monitors, and becomes aware of changes in bodily states (e.g., heart rate, fatigue, injury, arousal) to generate subjective feelings (e.g., disgust, interest, pain).

Six subcortical brain structures are highly relevant to motivational states. The striatum is located deep in the cortical brain and is central to the brain's reward center. The striatum consists of a dorsal part including the caudate (or caudate nucleus) and the putamen, and a ventral (or lower) part including the nucleus accumbens (NAcc). Together these three striatal structures are the brain's reward center (i.e., the hedonic evaluation of environmental stimuli). The ventral tegmental area (VTA) is the manufacturing site for brain dopamine, which is the neurotransmitter information that stimulates the brain's reward center. Activation of the VTA-to-striatum pathway allows people to learn the reward value of environmental objects and events. The hypothalamus is a very small brain structure that is nevertheless a motivational giant, because of its central role is biological motivations such as hunger, thirst, satiety, and sex. The hypothalamus also regulates both the endocrine system (hormonal) and the autonomic nervous system (arousal). The amygdala is another core motivational brain structure, as it detects, learns about, and responds to emotionally significant and aversive events. In doing so, it generates intense negative emotionality such as fear, anger, and anxiety as well as defensive behaviors such as freezing.

The human brain is massively interconnected. Bi-directional neural pathways extend from all brain structures identified above, to the extent that a change in one structure leads to changes in its connected brain structures. For instance, activation of the amygdala can lead to negative emotionality and pessimistic expectations in the prefrontal cortex, while activity in the prefrontal cortex (e.g., an emotion regulation strategy, such as reappraisal) can modulate and calm that amygdala activity. Because the human brain is so massively interconnected, motivation researchers often study integrated brain circuits, and the next section overviews the three most studied motivation-centric brain circuits – namely, the reward circuit, the valuation pathway, and the self-regulation/self-control network (Kim, 2013; Rangel, Camerer, & Montague, 2008).

THREE CORE BRAIN CIRCUITS

One of the fundamental questions regarding the neuroscience of motivation is what neural mechanisms underlie the selection, energization, maintenance, and modification of an action. There is accumulating neuroscientific evidence that motivation-related brain regions can be categorized into three distinct neural networks: reward-driven approaches, value-based decision-making, and goal-directed control (Kim, 2013; Rangel et al., 2008).

Reward directly drives our initial approach or seeking behavior toward incentives. The reward circuit is a process in which an approach behavior is triggered dependent on incentive salience. It is also implicated in the learning of stimulus-action-reward associations. Value guides our actions by highlighting those options that maximize utility. The valuation pathway involves value-based decision-making process that represents value, evaluates various outcomes of certain actions, and constantly recalculates and updates existing values. Goals can guide our behavior toward an anticipated future reward. The goal-directed control network is engaged in the regulation of motivation through cognitive control. This system is associated with executive functions such as goal maintenance, performance monitoring (updating), and strategy selection (shifting).

System 1: The Reward Circuit

Most of our everyday behavior is shaped by reward, which can be defined as tangible or intangible external stimuli that lead to satisfaction. The brain mechanisms behind reward processing have been extensively studied, with many studies demonstrating that the neural circuit involved in reward processing is the mesolimbic dopamine pathway, including the ventral tegmental area (VTA), the amygdala, and the three core structures within the striatum – namely, the caudate, putamen, and nucleus accumbens (NAcc) (see Fig. 3).

The environmental cues that signify the opportunity to obtain a reward increase reward anticipation. Reward-predicting cues are motivationally salient, indicating the attentional relevance of a stimulus in terms of its capacity to drive a particular behavior. Greater reward anticipation would lead to a strong approach behavior toward the reward.

The ventral striatum is commonly activated during both the anticipation and the receipt of various kinds of reward, such as praise, loved ones, and music as well as food, drugs, and monetary incentives (Aron et al., 2005;

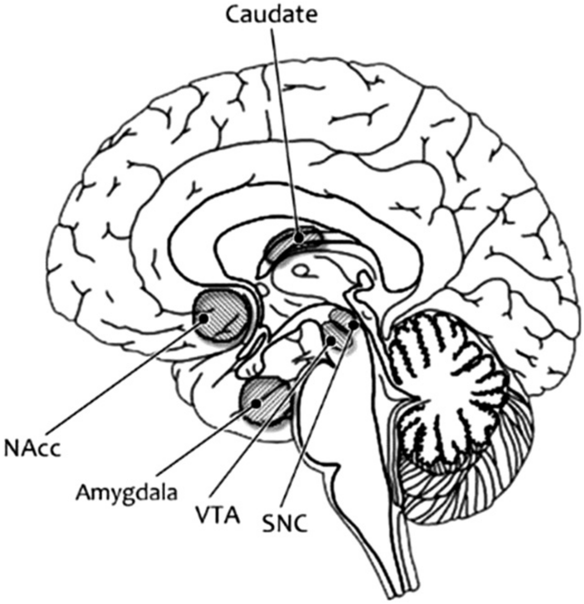

Fig. 3. The reward circuit. Brain regions activated by reward experiences include dopaminergic pathway (VTA, amygdala, caudate, and NAcc).

Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). However, a recent study demonstrated that dissociable neural networks are involved in reward anticipation and reward consumption (Rademacher et al., 2010). It was also found that activity in the ventral striatum more highly correlates with anticipated reward than actual reward per se (Knutson, Fong, Adams, Varner, & Hommer, 2001; O'Doherty, Deichmann, Critchley, & Dolan, 2002).

Unexpected rewards activate the ventral striatum more strongly than expected rewards. This is referred to as a reward prediction error, which is the discrepancy between the expected and actual reward (Schultz, 1997). More optimal learning occurs when reward prediction errors are greater. Thus, unexpected and surprising rewards would lead to reinforcement learning or feedback-based learning, whereas fully predicted rewards would not lead to learning.

Although the function of reward seems to be straightforward, reward processing is an intricate process involved in motivation, emotion, and learning. Berridge and colleagues (Berridge & Kringelbach, 2015; Berridge & Robinson, 2003) parsed the function of reward into three distinct components that have separate neural mechanisms: wanting, liking, and learning. Wanting is an incentive salience that drives an approach behavior toward a reward during the initial appetitive phase, whereas liking is pleasure or affective reactions to hedonic impact during the consummatory phase. The dissociation between wanting and liking suggests that motivation and pleasure may not covary.

Leotti and Delgado (2011) found that the anticipation of choice activated the ventral striatum. In addition, positive feedback such as praise that enhances competence recruits the reward circuit (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). A wealth of social neuroscience findings has demonstrated that the brain responds to social rewards including relatedness in the same way that it responds to tangible rewards (Bhanji & Delgado, 2014).

System 2: The Valuation Pathway

Behaviors are guided by value (Rangel et al., 2008), which can be defined as the quantification of the benefits or costs associated with any action or object (Louie & Glimcher, 2012). Human motivation can therefore be viewed as a series of value-based decisions that maximize expected value.

We constantly make decisions throughout the day, both big and small, such as choosing lunch, whether to watch TV or not, or a future career path. The choices made by an individual are a valid behavioral indicator of motivation. In fact, any choice or go/no-go decision begins the direction, vigor, and persistence of a behavior. Thus, the decision-making process plays a central role in motivation by selecting the action or object of highest value among several alternatives (Kim, 2013).

What brain systems are involved in prompting an organism to select a particular action? How is value represented, coded, compared, and updated in the brain? The neural basis of value-based decision-making is an extensive network of cortical and subcortical structures including the PFC, striatum, amygdala, and insula (Rangel et al., 2008). Among these, the orbitofrontal cortex (OFC) and the ventromedial prefrontal cortex (VMPFC) are the primary brain regions for the valuation process (see Fig. 4), including value representation, value calculation, and value learning (Grabenhorst & Rolls, 2011). A medial and lateral distinction within the OFC suggests that the medial OFC tends to encode appetitive value, whereas the lateral OFC encodes aversive value.

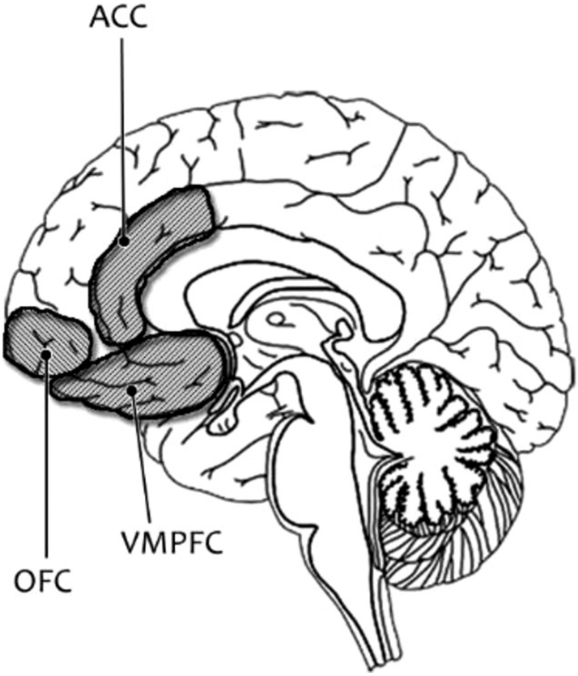

Fig. 4. The valuation pathway. Brain regions involved in the value-based decision-making process include OFC, vmPFC, and ACC.

The OFC is activated when individuals anticipate value, evaluate the value of an outcome, and learn a new value (Bartra, McGuire, & Kable, 2013; Jones et al., 2012). Numerous *f*MRI studies have also shown that activities in the OFC correlate with subjective value, desirability, and preference for an option, indicating that a neural signal in the OFC, the so-called "common neuronal currency," represents value (Padoa-Schioppa & Assad, 2006). The notion of a single currency which guides decision-making has been widely accepted in neuroeconomics research (Montague & Berns, 2002).

Defining motivation as value-based decision-making has a great deal of utility from both theoretical and practical perspectives. If we can understand the dynamics of value-based decision-making process, a range of motivation-related phenomena, such as incentive motivation, learning, and self-regulation, would be explained parsimoniously in terms of a single overriding value construct. In the design of motivation-enhancement intervention programs, value learning and decision-making training could be included.

System 3: The Self-Regulation/Self-Control Network

Many desires, impulses, strivings, urges, wants, needs, and strong emotions are generated in the subcortical brain. They often have a short-term (but urgent) timescale. In contrast, many motivational phenomena studied in educational psychology are cortical, longer-term goal strivings. A goal is an anticipated future reward or a desired state toward which behavior is directed. When tempting urges compete with a goal, how do people regulate their motivation toward the goal? Impulsive actions or choices are the result of failures in motivation regulation. A simple way of regulating motivation is by suppressing impulses. However, even this simple inhibitory mechanism is modulated by cognitive control, which is guided by the goal. Goal-directed control requires higher-order cognitive control which overlaps with metacognitive processes (Fleming & Dolan, 2012) and executive functions, including monitoring, shifting, and updating sub-processes (Miyake et al., 2000).

Two core brain regions involved in the cognitive control process are the ACC and the dorsolateral prefrontal cortex (DLPFC) (see Fig. 5). The ACC is activated when performance is monitored and an error or conflict is detected (Botvinick, Cohen, & Carter, 2004), whereas the DLPFC is responsible for working memory and executive functions (Miller, 2000). When two choices of reward – immediate-small or delayed-large – are given, humans tend to prefer immediate over delayed reward due to temporal or delay discounting. Brain imaging research into the neural mechanisms underlying intertemporal choice suggests that the choice of immediate reward increases ventral striatum activity, whereas the choice of delayed reward is associated with the DLPFC activation (Kable & Glimcher, 2009; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007).

Consistent with its key role in goal representation and manipulation in working memory (Miller & Cohen, 2001), the DLPFC, which modulates the value signal encoded in the OFC, is implicated in a wide range of goal-directed control processes, such as self-control (Hare, Camerer, & Rangel, 2009), emotion regulation (Ochsner & Gross, 2005), and general intelligence (Deary, Penke, & Johnson, 2010). The DLPFC has widespread projections and exerts top-down control over other brain regions such as the basal ganglia and the ACC (Miller, 2000). Therefore, the main function of the neural circuitry mediating goal-directed control is to maintain goal-relevant information and to plan and monitor the process of achieving it.

In Hare et al. (2009)'s study, participants' brain activation was measured during a choice between healthy versus tasty food, a decision in which

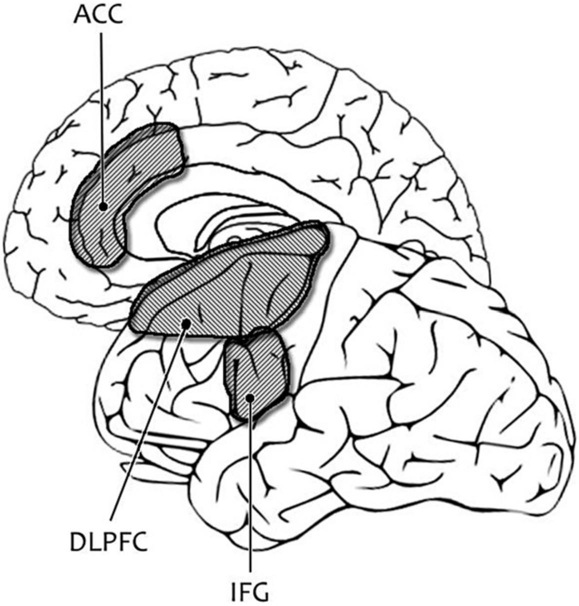

Fig. 5. The self-regulation/self-control network. Brain regions implicated in goal-directed control include ACC, DLPFC, and IFC.

self-control requires refusal to eat tasty but unhealthy food. The results showed that the ventromedial PFC (vmPFC: part of the OFC) encoded both the taste and health value of food in self-controllers but only that for taste in non-self-controllers. Greater activation in the DLPFC was found in the self-controlling group (i.e., successful dieters) than in the non-self-controlling group (i.e., unsuccessful dieters) and during successful self-control trials compared with failed trials. In addition, the strong functional connectivity between the vmPFC and the DLPFC in self-controllers indicated that the DLPFC modulated the vmPFC during self-control.

There is marked individual variability in the structure and function of the DLPFC as well as in self-regulation capability. Those with a high working memory capacity exhibit greater ability to delay gratification and resist temptation in the intertemporal choice between immediate-small and delayed-large reward (Shamosh et al., 2008). Walter Mischel and colleagues followed up the participants in their famous "Marshmallow Experiment" 40 years later (Casey et al., 2011). They found that those who had been successful in delaying their gratification (i.e., high delayers) displayed greater activation in the PFC during the suppression of responses to alluring cues than those who had failed to resist the temptation (i.e., low delayers). Thus, both behavioral and imaging evidence suggests that high delayers use their working memory more actively to control impulses by maintaining current task goals in their working memory.

CONCLUDING REMARKS

There are two different approaches to integrating neuroscience into other disciplines. First, neuroscience can complement, enrich, and strengthen the discipline, and it can do so in a cooperative and synergistic way. Second, neuroscience can challenge and debate against the discipline, by casting doubt on that discipline's basic assumptions and concepts. This is a more competitive and "survival of the fittest" or "us versus them" approach.

The present volume is an effort to advance the former approach (cooperative) and to avoid the latter (us vs. them) approach. Neuroscience can add fresh perspectives, introduce new objective sources of data, and provide a level of understanding that is not really possible in the absence of a neuroscientific analysis. To help readers better see (and appreciate) the contribution that neuroscientific data can add to the contemporary motivation study, this volume gathers excellent contributions from leading researchers in the field of motivational neuroscience and is dedicated to advancing our understanding of the brain mechanisms underlying various motivational phenomena, including reward, approach, value, goals, autonomy, intrinsic motivation, learning and memory, feedback, effort, curiosity, engagement, self-control, and individual differences.

This volume is divided into four sections. The first section introduces classical but fundamental issues in motivation such as reward, approach, and individual differences. The second section deals with intrinsic motivation including autonomy and curiosity. While reading these six chapters, we encourage the reader to recall Fig. 3 and the brain structures that make up the reward circuit. The third section examines recent approaches to the interface between motivation and cognition in learning and decision-making. While reading these three chapters, we encourage the reader to recall Fig. 4 and the brain structures that make up the valuation pathway. The last section focuses on significant practical issues pertaining to engagement and self-regulation. While reading these three chapters, we encourage the reader to recall Fig. 5 and the brain structures that make up the self-regulation/self-control network. We hope, after having read this volume, the reader develops an appreciation for the potential contribution neuroscience can make to our understanding of human motivation.

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PART I
REWARD AND APPROACH

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NEUROSCIENCE OF REWARD, MOTIVATION, AND DRIVE

Morten L. Kringelbach and Kent C. Berridge

ABSTRACT

Drive and motivation are central to affective neuroscience. Here, we describe the development of conceptualizations from early behaviorist theories to contemporary theories linking motivation closely to reward. Current experimental data suggest key roles of drive and motivation in the wanting, liking, and learning processes underlying the pleasure cycle supporting survival of individuals and species. In particular, the underlying functional neuroanatomy of drive and motivation is now becoming clearer in humans and other mammals, which provides hope for novel more effective interventions for the pervasive problems of drive and motivation in affective and addictive disorders.

Keywords: Motivation; pleasure; brain; addiction

INTRODUCTION

There is a long history in psychology and neuroscience of considering concepts of motivation and drive to understand our behavior; in particular to help better understand the variability of behavior as well as the short-term

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stability of goal-directed and threat-avoidant behaviors (Berridge, 2004). The main goals of this research have been trying to answer important questions of (1) why do individuals react to affectively important stimuli, (2) why do the individuals seek out specific things at particular times, and (3) why do the individuals choose to do different things at different times when faced with identical and constant stimuli?

Initially, progress was slow to adequately address these complex questions but over the last two decades affective neuroscience has made significant progress possible for understanding how motivation is driven by interactions over time between specific networks in the brain. In particular, it has become clear how motivation plays a significant role in the pleasure cycles that help allocate the necessary brain resources for behaviors promoting survival (Fig. 1) (Berridge & Kringelbach, 2008). In addition, we now have much better understanding of the functional neuroanatomy of underlying wanting, liking, and learning processes which have been linked

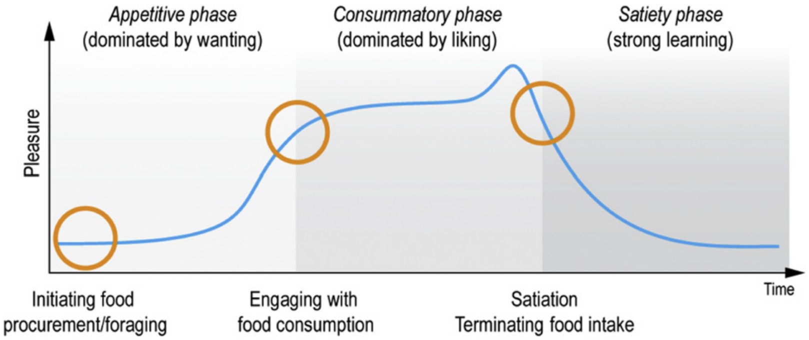

Fig. 1. The Pleasure Cycle. *Notes*: The cyclical processing of rewards has classically been proposed to be associated with appetitive, consummatory, and satiety phases (Craig, 1918; Sherrington, 1906). Research has demonstrated that this processing is supported by multiple brain networks and processes, which crucially involves *liking* (the core reactions to hedonic impact), *wanting* (motivational processing of incentive salience), and *learning* (typically Pavlovian or instrumental associations and cognitive representations) (Finlayson, King, & Blundell, 2007; Robinson & Berridge, 1993, 2003). These components wax and wane during the pleasure cycle and can co-occur at any time. Importantly, however, wanting processing tends to dominate the appetitive phase, while liking processing dominates the consummatory phase. In contrast, learning can happen throughout the cycle.

to dissociable networks of specific subcortical and cortical regions (Berridge & Kringelbach, 2015).

Here, we first briefly review a number of early behaviorist theories of drive and motivation and discuss their relative merits. We then turn our attention to contemporary theories linking motivation closely to reward, which have overturned earlier, erroneous theories proposing that drive reduction supposedly was the chief mechanism of reward. We show how the current experimental data suggest a key role of motivation in the wanting, liking, and learning processes underlying the pleasure cycle. In particular, we sketch the underlying brain circuitry supporting these processes over time.

EARLY THEORIES OF HOMEOSTATIC DRIVE

In the 1920s, drawing heavily on the earlier work by Claude Bernard and others physiologists, Walter Cannon developed the idea of *homeostasis* as the ability to maintain a stable internal state (Cannon, 1932). Subsequent research came to regard homeostasis as a specific type of regulatory system that uses a setpoint or built-in goal value to maintain a stable physiological state. Constant comparisons between the current setpoint and the desired physiological state drive a mismatch regulator triggering a homeostatic mechanism for the correction of the current state. The temperature thermostat found in many homes is often used as a simple analogy of this principle, yet presumably homeostasis in the human body must have many more error detectors. Thus homeostasis for, say, hunger, would entail error detectors embedded in neural, hormonal, and physiological systems with setpoints, for example, body weight, blood glucose, nutrient storage, neural metabolism, and other physiological variables relevant for hunger and satiety. Such ideas have dominated the behavioral neuroscience of hunger, thirst, salt appetite, and other ingestive behaviors. Following this view, a better understanding of motivation and problems with motivation is simply a question of a more detailed understanding of homeostatic-deficit triggers and their receptors. Much interesting research has arisen from this, yet it has also become clear that homeostatic drive cannot alone account for many known problems such as our current pandemic of obesity (Kringelbach, 2004).

Instead, it has been become clear that what may appear to be a homeostatic balancing of physiological systems can be achieved without homeostatic setpoints mechanisms, for example, through the use of anticipatory mechanisms (Fitzsimons & Le Magnen, 1969; Schulkin, 2003) (i.e., drinking and eating in anticipation of hunger and thirst) or through "settling points" (i.e., a stable balance between opposing forces) (Wirtshafter & Davis, 1977). Take the example of obesity, which is difficult to explain as a purely homeostatic drive (Bolles, 1980; Kringelbach, 2004). The homeostatic theory would hold that the regulation of eating behavior requires a body weight setpoint from which hunger would be triggered. Yet, such a setpoint has not been found. Instead, it would appear that body weight simply settles around a moderately stable point settled by many factors, including internal appetite and satiety mechanisms as well as availability and palatability of foods. In other words, the pleasure of food can lead to overeating in the absence of a homeostatic deficit (Kringelbach, 2004).

Interestingly, Cannon never actually wrote about homeostasis in terms of setpoints, setpoint comparisons, or error detection. These concepts instead came from cybernetic theories in engineering and computer science (Wiener, 1948). Cannon thought about homeostasis exclusively in terms of opposing reflexes, for example, a high stimulus triggered an internal reflex which reduced the stimulus and restored homeostasis, that is, essentially as a settling point rather than a setpoint.

Another way to think about drive and motivation came with the rise of behaviorism, where behaviorists were obsessed with only describing behavior in terms of observable stimuli and responses. However, this quickly gives rise to ever more complex relationships when adding mappings between more stimuli and responses. One way to simplify these relationships is to introduce drive as an intervening variable, where, for example, by adding thirst as an intervening variable, this becomes a common route through which stimuli and responses can be mapped. This is meant to be a purely objective relationship, yet it is also clear from the data that thirst can have very different effects on responses.

FLEXIBLE GOALS AND AFFECTIVE DISPLAYS

Rather than continuing with the fairly sterile behaviorist concept of drive and motivation as intervening variables, researchers began to explore the idea of *internal* motivational processes. In the 1960s and early 1970s Philip Teitelbaum suggested one interesting way to think about real motivation as that which helps to motivate flexible instrumental behavior

(Teitelbaum, 1966, 1977). This built on the insights from the beginning of the 20th century, where ethologists and physiologists such as Craig, Sherrington, and others had proposed that all motivated behavior can be divided into two sequential phases: an appetitive phase and a consummatory phase (Craig, 1918; Sherrington, 1906). The appetitive phase of motivated behavior contains the flexible approach behavior that an individual emits before the motivational goal is found. Similarly, the consummatory phase follows consisting of stereotyped and species-specific patterns, whether for ingestive behaviors or sex and aggression. Teitelbaum drew attention to the appetitive phase as essential for motivation to drive the interaction with instrumental associative learning shaping new operant responses.

More generally, Epstein proposed that three additional criteria are needed to distinguish motivated behavior: (1) flexible goal directedness, (2) goal expectation, and (3) affect (Epstein, 1982). The first criterion builds on Teitelbaum's operant learning idea by emphasizing the need to rule out simple forms of learning and simple drive activation of behavior. While instrumental learning is interesting, it is still much less complex than, for example, cognitive inferences. Similarly, various forms of expectation from classical conditioning of an anticipatory conditioned response to declarative, cognitive forms of goal expectation are central to motivation. Finally, Epstein proposed that real motivation is always accompanied by affective reactions to the goal itself. Motivation is always directed toward hedonically laden goals and the presence of hedonic reactions confirms that a given behavior is motivated.

Building on these insights, psychologist Richard Solomon proposed *opponent process theory* as a useful general concept for thinking about how many processes with different valences can interact (Solomon & Corbit, 1974). All hedonic stimuli elicit not only their own hedonic reactions but also an opponent process of opposite hedonic value, which helps maintain homeostasis. Yet, there are limits to the explanatory power of this theory in that the opposite processes do not occur for every affective event and are not always the chief motivational factor.

Another very popular concept in the history of motivational drives is the idea that *drive reduction* is the main mechanisms of reward (Hull, 1943; Mowrer, 1960; Spence, 1956). According to this concept – which in its day was seen so powerful as to be self-evident – food is a reward because it reduces hunger drive, while water is a reward because it reduces the thirst drive. Yet, the overwhelming evidence has clearly shown that this concept is false. Even for food and hunger, reducing physiological drive via intravenous feeding is not particularly effective at stopping eating (Epstein & Teitelbaum, 1962). Similarly, evidence from brain stimulation reward showed that stimulation of brain sites associated with eating behavior would almost always coincide with sites where stimulation was rewarding (Valenstein, Cox, & Kakolewski, 1970), rather than with a reduction of reward as posited by the drive reduction theory.

INCENTIVE MOTIVATION CONCEPTS

These findings instead led to a revival of the old idea from ancient Greek philosophers such as Aristotle that hedonic reward or pleasure is at the heart what motivates us. Early pioneers such as Pfaffmann argued that neural encoding of rewards such as sweet taste and sex must be rewarding and motivating in and of itself, without the need for drive reduction (Pfaffmann, 1960; Pfaffmann, Norgren, & Grill, 1977). Similarly, later researchers such as Stellar asserted the need for behavioral neuroscience to study affective reactions (Stellar, 1982).

The failure of various theories of homeostatic drive, intervening variables and drive reduction to explain real motivation coupled with the realization of centrality of pleasure for understanding motivation, led to the development of incentive motivation concepts during the 1970s and 1980s. First, Bolles argued that individuals are motivated incentive expectancies rather than by drives or drive reduction (Bolles, 1972). Such incentive expectancies are learned expectations of hedonic reward. Bindra furthered this concept by rejecting expectation per se as the important factor for incentive motivation for rewards (Bindra, 1974, 1978). Instead, Bindra proposed that a conditioned stimulus for a reward evokes the same incentive motivational state caused by the reward, that is, it becomes a reward in and of itself. Toates then added to this concept by suggesting that physiological depletion states can enhance incentive motivation for appropriate incentives and cues (Toates, 1986). According to the theories of incentive motivation, individuals will select the available reward with the highest incentive value.

These concepts fit well with the alliesthesia concept coined by Michel Cabanac showing that physiological states can modulate the perceived hedonic value of rewards (Cabanac, 1971, 1979), for example, how a warm bath is delicious when we are cold but not on a very hot day.

Adapting these insights, Berridge and colleagues realized in the 1990s that the incentive motivation value of reward can be further split into incentive salience, "wanting" and the hedonic impact, "liking" with partly dissociable brain networks and neurotransmitters (Berridge, 1996; Berridge, Venier, & Robinson, 1989). Incentive salience makes a hedonic reward more attractive, attention grabbing, and ultimately available for Bindra-Toates goal-directed strategies. This is different from the hedonic impact, which triggers the brain reaction to pleasure. Normally, "liking" and "wanting" relate the same incentive value, but there are situations where they are different. It is possible, for example, to have "wanting" without "liking" as was the case for brain stimulation, where, for example, stimulation of the lateral hypothalamus in rats would trigger motivated eating behaviors without the associated hedonic face expressions (such as licking) associated with eating in rats (Berridge & Valenstein, 1991).

One important further insight from this body of research is the *incentive-sensitization theory of addiction* (Robinson & Berridge, 2003), which combines neural sensitization of dopamine-related brain systems with incentive salience to propose that sensitized "wanting" may explain compulsive long-lasting addiction and relapse. Many addictive drugs, such as cocaine, heroin, amphetamine, nicotine, and alcohol, cause neural sensitization in brain mesocorticolimbic systems which can trigger the brain systems into both sensitization (through increase in dopamine release) and tolerance (through decrease in dopamine receptors). The tolerance mechanisms usually recover within days whereas neural sensitization can last for years (Paulson, Camp, & Robinson, 1991). This may explain why some addicts may not like drugs but still want them, and why the relapse can occur in the context of drug-associated cues such as paraphernalia or places and social settings. We are thus beginning to understand why motivation and unbalancing of the associated brain networks can have devastating consequences but these insights also open up for the development of potential new treatments.

A growing body of evidence has started to map the underlying brain networks and transmitters involved in parsing reward in the pleasure cycle, linking "wanting," "liking," and "learning." This affective neuroscience endeavor has mapped "wanting" processes to changes in dopamine, which is not related to the "liking." On the other hand, "liking" processes have been linked strongly with opioids. In terms of brain regions, wanting for rewards is generated by a large and distributed brain system, while "liking" is served by a much smaller set of discrete hedonic regions with pleasure hotspot and coldspot regions in subcortical areas of the brain such as the nucleus accumbens and ventral pallidum (Peciña & Berridge, 2005; Smith & Berridge, 2007) (Fig. 2). Manipulations of these regions with opioids have been shown to causally change pleasure-elicited reactions (Berridge & Kringelbach, 2013).

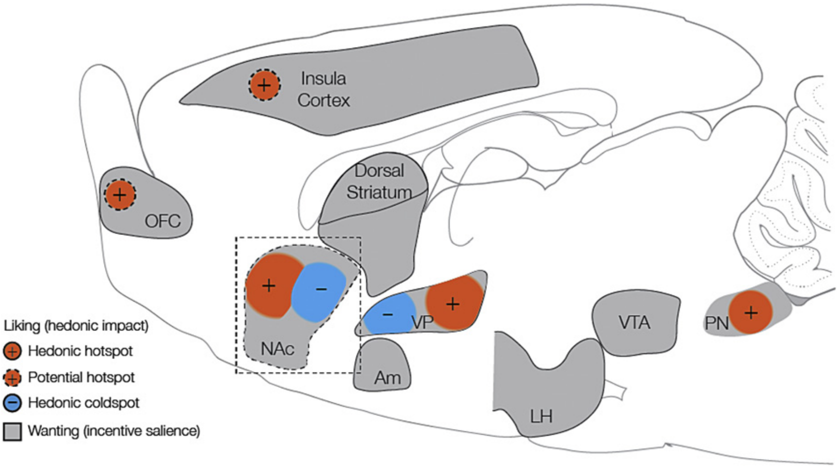

Fig. 2. Liking and Wanting Circuits in the Rat Brain. *Notes:* The figure shows sagittal view of wanting (incentive salience, in gray) and liking (hedonic impact) regions in the rat brain. The large spread wanting regions include dorsal striatum, lateral hypothalamus (LH), ventral tegmental area (VTA), parabrachial nucleus (PN), amygdala (Am), nucleus accumbens (NAc), ventral pallidum (VP), insula cortex, and orbitofrontal cortex (OFC). Within these regions there are hedonic hotspots in much smaller regions of NAc, VP, and PN, as well as, putatively, insula cortex and OFC. Hotspots (+) depict sites where opioid stimulation enhances “liking” reactions elicited by sucrose taste (with a stippled line indicating putative hotspots). Coldspots (−) show sites where the same opioid stimulation oppositely suppresses “liking” reactions to sucrose.

Other regions involved in wanting and liking have been found using human neuroimaging in the orbitofrontal, cingulate, medial prefrontal, and insular cortices (Amodio & Frith, 2006; Berridge, 1996; Cardinal, Parkinson, Hall, & Everitt, 2002; Everitt & Robbins, 2005; Kringelbach, 2010; Kringelbach, O’Doherty, Rolls, & Andrews, 2003; Kringelbach & Rolls, 2004; Watson, Shepherd, & Platt, 2010). These interacting networks do not act in splendid isolation but are embedded within much larger brain networks (Fig. 3). We are beginning to understand the metastable nature, topological and functional features of these networks using advances in network science and graph theory together with advanced whole-brain computational models (Cabral, Kringelbach, & Deco, 2014; Deco & Kringelbach, 2014; Kringelbach, McIntosh, Ritter, Jirsa, & Deco, 2015).

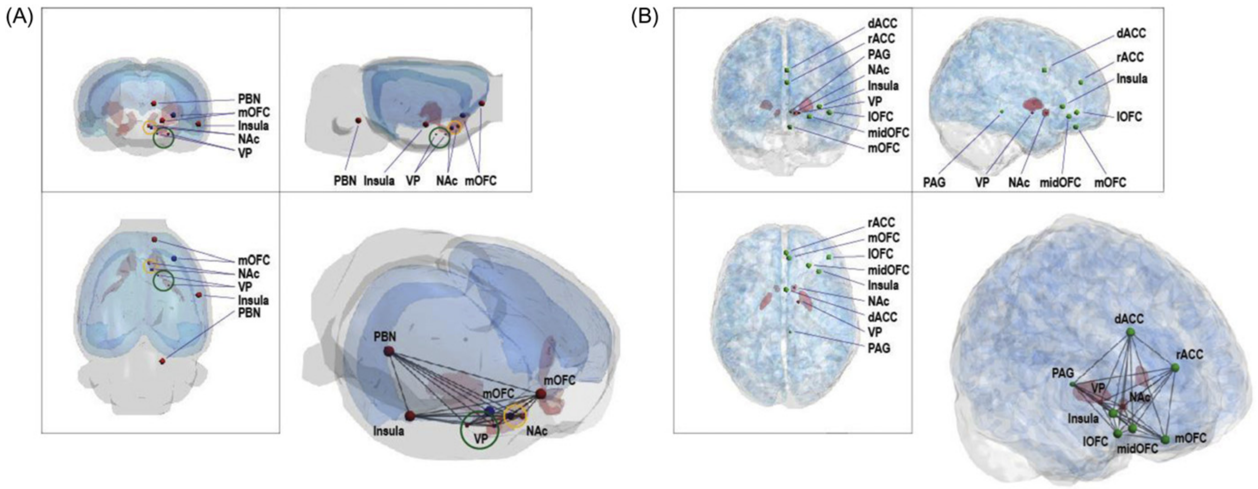

Fig. 3. Three-Dimensional Comparison of Hedonic Sites in Rat Brain (Left) and Human Brain (Right). *Notes:* (A) Rat brain shows hedonic hotspots (+) and coldspots (–) in coronal, sagittal, horizontal planes, and in 3D fronto-lateral perspective view (clockwise from top left). (B) Human brain shows extrapolation of rat causal hotspots to analogous human sites in NAc and VP (+), and shows fMRI coding sites for positive affective reactions in green (from text). Human views are also in coronal, sagittal, horizontal, and 3D perspective (clockwise from top left of B). The tentative functional networks between the different hotspots and coldspots have been added to give an impression of the topology of a pleasure network. The functional connection lines are not meant to imply direct anatomical projections between two connected structures, but rather a functional network in mediating hedonic "liking" reactions and subjective pleasure ratings. Abbreviations: VP, ventral pallidum; NAc, nucleus accumbens; PBN, parabrachial nucleus; mOFC, medial orbitofrontal cortex; lOFC, lateral orbitofrontal cortex; midOFC, mid-anterior orbitofrontal cortex; dACC, dorsal anterior cingulate cortex; rACC, rostral anterior cingulate cortex; PAG, periaqueductal gray.

CONCLUSION

Over the last century much progress has been made in understanding motivation in the human brain (Kringelbach & Berridge, 2010). Fascinating new insights have tied motivation closely the pleasure system of the brain and it has become clear that "wanting," "liking," and learning processes are carefully choreographed in the healthy human brain. Through this careful, growing body of brain research, we now have a much clearer idea about why individuals react to affectively important stimuli, as well why they seek out specific things at particular times and why they choose to do different things at different times when faced with identical and constant stimuli. We are beginning to understand how unbalancing of these processes can lead to the diverse symptoms of anhedonia found in affective disorders (Rømer Thomsen, Whybrow, & Kringelbach, 2015). Ultimately, carefully characterizing the interactions between brain networks involved in motivation during a healthy pleasure cycle may come to offer new, early biomarkers for affective disorders and perhaps novel, more effective interventions in the years to come.

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ON THE NEUROSCIENCE OF APPROACH AND WITHDRAWAL MOTIVATION, WITH A FOCUS ON THE ROLE OF ASYMMETRICAL FRONTAL CORTICAL ACTIVITY

Douglas Jozef Angus and Eddie Harmon-Jones

ABSTRACT

Extensive human and animal research has examined approach and withdrawal motivation, which we define as the simple urge to move toward or away, respectively. In this chapter, we review seminal and recent research that showing that asymmetrical frontal cortical activity underlies approach and withdrawal motivation that occur during childhood, that characterize certain psychopathologies, and are present in everyday emotional experiences. Specifically, greater left-frontal activity is involved in approach motivation, including the expression and experience of anger, jealousy, desire, and joy. Conversely, greater right-frontal activity is involved in withdrawal motivation, including the expression and experience of some forms of sadness, crying, and depressed mood. We also review recent research suggesting that connectivity between the

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frontal and parietal cortices is a potential mechanism for the motivation-related effects of asymmetrical frontal activity.

Keywords: Anger; EEG; approach motivation; withdrawal motivation

The notion of brain lateralization is widely represented in lay conceptions – and misconceptions – of brain function. Common [mis] interpretations often focus on vague representations of "left brain" versus "right brain" differences in personality, which have extremely limited empirical or theoretical support. Yet, these misconceptions have a hidden grain of truth, insomuch that lateralized brain *activity* is involved in functionally different motivational responses. Extensive research over the past 30 years has provided considerable evidence that leftward asymmetrical activity in the frontal cortex is functionally related to *approach motivation*, while rightward asymmetrical activity is functionally related to *withdrawal motivation* (for reviews of the history of this research, and the development of the approach/withdrawal perspective, see Davidson, 2004; Fox, 1991; Harmon-Jones, Gable, & Peterson, 2010).

Approach and withdrawal motivation are often viewed as independent constructs rather than as the end points of a bipolar continuum (Cacioppo & Berntson, 1994; Ito & Cacioppo, 1999). However, whether approach and withdrawal motivation are organized in an independent or bipolar fashion likely depends on how intense the motivation is, or how close the motivation is to actually implementing behavior. In other words, at lower levels of motivational intensity, approach and withdrawal may operate independently, such that an organism can be high in both approach and withdrawal motivation. However, at higher levels of motivational intensity, approach and withdrawal operate in a bipolar fashion, such that an organism can only be high in one motivational direction and low in the other. In our view, the relationship between frontal asymmetry and approach and withdrawal motivation reflects facets of motivation that are very close to their actual behavior implementations (e.g., reaching toward a desired object or withdrawing from social situations).[1]

This chapter focuses on recent literature linking asymmetrical frontal cortical activity to approach and withdrawal motivation. First, we provide an overview of the basic physiology and measurement of this activity.

Then, we discuss research on *trait-level* relationships between frontal asymmetry and motivational direction and intensity, and research that examines the effect of "global" environmental variables on frontal asymmetry – time of day and time of year. Then, we discuss *state-level* relationships between frontal asymmetries and motivation. As we discuss in more detail, these state-level relationships have been found to be bidirectional, with increases in cortical asymmetry enhancing approach or withdrawal motivation, and exposure to stimuli or events that produce approach or withdrawal being associated with an increase in left or right hemispheric asymmetry, respectively. Finally, although much less extensive, the growing literature on parietal and frontal-parietal asymmetries and motivation will also be briefly reviewed.

WHY ASYMMETRICAL FRONTAL CORTICAL ACTIVITY?

Interest in the roles of the left- versus right-frontal cortical regions in emotional and motivational phenomena was originally spurned from observations of individuals who had suffered damage to one of these regions. That is, individuals who had suffered damage to the left-frontal cortex were likely to develop depressive symptoms following the lesion, whereas individuals who had suffered damage to the right-frontal cortex were likely to develop manic symptoms following the lesion. Combined with other research, scientists suggested that the emotive outcomes occurred because the emotive functions of the non-damaged hemisphere were over-expressed when no longer inhibited by the other damaged hemisphere. In other words, when the left-frontal cortex was damaged, the emotive functions of the right-frontal cortex were expressed in an extreme degree. Thus, these scientists suggested that the right-frontal cortex was involved in the expression and experience of negative affect. Conversely, when the right-frontal cortex was damaged, the emotive functions of the left-frontal cortex were expressed in an extreme degree. Thus, the left-frontal cortex was involved in the expression and experience of positive affect.

These observations with humans were also consistent with observations of lateralization of emotive functions in non-human animals. That is, a large body of evidence has suggested that a wide range of species show lateralization of emotive function similar to those observed in humans. However, some of these species lack much of a frontal cortex, suggesting that this lateralization of function is evolutionarily old and may have “migrated” to the frontal cortex of humans.

A BRIEF INTRODUCTION TO FRONTAL ALPHA ASYMMETRY

Before we review the research that has used frontal asymmetry as a predictor or outcome variable, we first provide a brief overview of what frontal asymmetry refers to and its physiological basis. One of the primary measures used in research on asymmetrical frontal cortical activity and motivational direction is referred to as frontal alpha asymmetry. This refers to hemispheric differences in the amplitude of electroencephalographic (EEG) oscillations that are measured across anterior regions of the scalp, and within the frequency band of between 8 and 13Hz. Although there is debate about what alpha band activity represents at a neuroanatomical level (Klimesch, Sauseng, & Hanslmayr, 2007), research utilizing Positron Emission Tomography (Cook, O’Hara, Uijtdehaage, Mandelkern, & Leuchter, 1998), and behavioral methods (Davidson, Chapman, Chapman, & Henriques, 1990) have shown that greater alpha activity reflects *decreased* levels of cortical activity, whereby smaller alpha band amplitudes reflect increased cortical activity.

With respect to *frontal* activity, differences in hemispheric activity levels are commonly interpreted as reflecting the reciprocal inhibition of one hemisphere by the other, such that relatively greater activity in one hemisphere reflects its inhibition by the other (Schutter & Harmon-Jones, 2013). This reciprocal inhibition is thought to occur via anterior regions of the corpus callosum, and takes three non-mutually exclusive forms. Firstly, one hemisphere activity can inhibit activity in the other, putatively to reduce conflict in outputs (*interhemispheric suppression*). Secondly, the hemispheres may become functionally decoupled by the corpus callosum, with processing within each hemisphere occurring normally but independent of one another (*interhemispheric isolation*). Thirdly, conflicting information can be transmitted from one hemisphere to the other, reducing the capacity for processing in the receiving hemisphere (*interhemispheric interference*). Although early studies examining alpha asymmetry often focused on the relative contribution that each hemisphere makes to behavior (Fox, 1994), more recent studies typically focus on *relative differences* in activity. The primary measures derived from frontal alpha asymmetry typically take the form of asymmetry scores or metrics, in which the amplitude of alpha activity recorded over the left hemisphere is subtracted from the amplitude of activity recorded over the right hemisphere. Because of the inverse relationship between alpha power and cortical activity, larger values indicate greater left hemispheric activity, while smaller – and negative values – indicate greater right hemispheric activity (Allen, Coan, & Nazarian, 2004). It is important to note that the specific mechanism underlying these relative differences in hemispheric activity (e.g., forms of callosal inhibition) is largely opaque to the methods used to examine frontal asymmetry.

The first wave of research on asymmetrical frontal cortical activity was guided by the conceptual idea that greater relative left-frontal activity was associated with positive affect, whereas greater relative right-frontal activity was associated with negative affect (Davidson, 1984; Heller, 1990). Subsequent research shows that this relationship between frontal cortical asymmetry and affect is driven by a natural confound between the motivational direction and intensity of these responses and their affective valance (Harmon-Jones, 2003). That is, positive and pleasant emotional states are predominantly associated with approach motivation, while negative and unpleasant states are predominantly associated with withdrawal motivation.

In many affective and motivational contexts, an affective valence conceptualization provides sufficient, albeit course-gained, explanation of the psychological constructs that frontal asymmetry likely represents. However, because some affective variables violate this confound, more precise examinations of the processes that alpha asymmetry captures were needed. A program of research conducted in our laboratory examining the relationship between alpha asymmetry and anger has shown that rather than reflecting processes specific to positive and negative affect, alpha asymmetry is more closely related to approach and withdrawal motivation. Anger violates the natural confound of affective valence and motivational direction, insomuch that it is typically associated with negative affect but also associated with approach motivation (Carver & Harmon-Jones, 2009a, 2009b).

In one study, Harmon-Jones and Allen (1998) examined the correlation between frontal asymmetry and trait anger measured using a well-validated self-report measure, the Buss-Perry Aggression questionnaire (Buss & Perry, 1992). Consistent with the approach/withdrawal conceptualization of frontal asymmetry, greater left-frontal asymmetry was positively correlated with greater self-reported trait anger. An alternative explanation for this effect is that particularly angry individuals perceive the energizing aspects of anger as positive, and consequently perceive anger itself as a positive affect. To test this idea, Harmon-Jones (2004) examined whether frontal asymmetry still predicted individual differences in anger while statistically controlling for individuals' attitudes toward anger. Importantly, the correlation between frontal asymmetry and trait anger held, even when positive – or negative – attitudes toward anger were statistically controlled. That is, the extent to which frontal activity predicts behavioral and physiological responses to affectively and motivationally salient events is context specific, and does not necessarily follow a simple rubric where left-frontal activity is inherently good, and right-frontal activity is inherently bad. Additional evidence for a link between approach-related forms of anger and leftward alpha asymmetry also comes from studies that manipulate emotional and/or cortical state, which we review later in this chapter.

TRAIT-LEVEL RELATIONSHIPS WITH MOTIVATION

The most commonly deployed investigative method in the alpha asymmetry literature has adopted a trait-level approach. This approach characterizes alpha asymmetry metrics obtained during resting or "neutral baseline" EEG recordings as reflecting stable measures of individual differences in prefrontal neural activity across the hemispheres. These metrics are then compared across groups (e.g., diagnostic subtypes), or used as variables in correlational analyses. This methodological approach has contributed greatly to our understanding of how frontal cortical asymmetries contribute to and underpin motivational variables in healthy, sub-clinical, clinical, and at-risk populations. In general, relative leftward asymmetries at rest have been associated with a proclivity to engage in or endorse approach-related phenomena, including aggression, reward seeking, and impulsivity, while relative rightward asymmetries at rest have been associated with withdrawal-related phenomena such as the experience of disgust and fear, depressive symptomology, internalization symptoms, and hormonal stress responses.

Developmental Studies

Some early observations indicated that alpha asymmetry metrics taken at rest were broadly reflective of individual differences in affective responses to emotionally provocative events. For instance, greater rightward asymmetry has been found to predict greater self-reported depression symptoms in adults (Schaffer, Davidson, & Saron, 1983). Subsequent research indicated that this effect generalized to other populations and emotional contexts, such as adult participants viewing films intended to evoke feelings of amusement and joy or disgust and fear. Consistent with developmental research, the extent to which participants reported negative affect during these films was predicted by frontal asymmetry, with greater rightward asymmetry predicting increased negative affect. Importantly, the predictive ability of frontal asymmetry in this context was found to be independent of how participants reported feeling at the time of the baseline recording (Tomarken, Davidson, & Henriques, 1990).

The application of this individual differences approaches to infants and young children revealed that these asymmetry effects can emerge as early as 10 months of age. The experience of maternal separation is particularly distressing for young infants, and early work on alpha asymmetry indicated that the manner in which infants responded to such an event was predicted by frontal asymmetry. Consistent with previous studies that had linked rightward asymmetries to unpleasant and withdrawal-related responses, greater rightward asymmetry was observed in infants who cried following separation than in those who did not cry (Davidson & Fox, 1989).

These early findings led to the wider application of alpha asymmetry in developmental contexts, with complementary lines of research finding that it serves as stable risk marker of dysfunctional and maladaptive approach and withdrawal behavior in children (Vuga, Fox, Cohn, Kovacs, & George, 2008). The development of symptoms involving behavioral withdrawal (e.g., internalization symptoms such as lethargy) has been related to relatively greater right-wards asymmetry, while the development of behaviorally active and approach-related symptoms (e.g., externalizing symptoms such as fighting with other children) has been related to relatively greater leftwards asymmetry (Gatzke-Kopp, Jetha, & Segalowitz, 2012).

Resting frontal activity has also been found to predict young children's affective responses in subsequent years. For instance, children's capacity to regulate their emotional response to stressful events at nine years of age has been found to be positively correlated with left-frontal activity at four and a half years of age (Hannesdóttir, Doxie, Bell, Ollendick, & Wolfe, 2010). The same study also found that autonomic arousal during social stress is inversely correlated with left-frontal activity, such that children with greater leftward asymmetry had slower heart rates and parasympathetic outflow then children with greater rightward asymmetry (Hannesdóttir et al., 2010). Similar affective and motivational findings have also been observed in adult populations. Greater right-frontal activity has been found to uniquely predict attention biases toward faces with angry facial expressions, even when statistically controlling for the possible state mood effects (Miskovic & Schmidt, 2010). Intriguingly, although frontal activity also predicted attentions biases toward happy faces, this was dependent on individual differences in parasympathetic outflow to the heart. In individuals who had high levels of parasympathetic outflow, which is typically interpreted as reflecting a greater capacity to adapt to changing attentional demands (Thayer & Lane, 2009), right-frontal activity was associated with *avoidance* of happy faces, and left-frontal activity was associated with attention biases toward these same faces (Miskovic & Schmidt, 2010).

Relationships with Psychological Disorders

The approach/withdrawal conceptualization of alpha asymmetry has also yielded important insights into one candidate for affective and motivational dysfunction in adult populations. Greater rightward asymmetry – suggestive of withdrawal motivation – has been correlated with a diagnosis of depression, difficulty of recovery, and duration of depressive episodes (for a recent review of this literature, see Allen & Reznik, 2015). This relationship has been observed using measures of average activity over a nominal timeframe (e.g., 4 minutes) and using transient bursts in asymmetry (Allen & Cohen, 2010), with the latter accounting for a disproportionally large amount of variance in the former.

Despite broadly consistent findings with respect to major depression, the role of rightward alpha asymmetry in other depression subtypes is more nuanced. Previous research suggests that the relationship between alpha asymmetry and depression is specific to the type of depression, with greater resting leftward asymmetry occurring in bipolar individuals during their manic phase relative to individuals with unipolar depression (Kano, Nakamura, Matsuoka, Iida, & Nakajima, 1992). Such findings have been interpreted as reflecting a neural basis for the excessive approach-related motivation that is observed during hypomanic phases of bipolar depression (Harmon-Jones et al., 2008). Indeed, recent research has reported that greater left-frontal activity predicts subsequent diagnosis of more extreme forms of bipolar disorder in individuals with less extreme forms of bipolar disorder (Nusslock et al., 2012). These results suggest that in individuals already experiencing hypomania, a proclivity toward excessive approach motivation at a neural level may act as a catalyst for the development of more severe dysfunction.

Frontal asymmetry has also been found to predict excessive manifestations of approach-related behavior, such as decreased effortful, supervisory control. In a recent novel study, Gable et al., (2015) examined how resting measures of frontal asymmetry predicted individual differences in "Positive Urgency," a self-report scale developed to index the endorsement of and engagement in impulsive behaviors that occur during positive emotion states. These types of behaviors occurring during positive states can result in maladaptive outcomes. Importantly, not only was frontal asymmetry positively correlated with increased positive urgency, but source-localization of this effect indicated that it was largely due to *decreased* activity in the right inferior frontal gyrus. This finding may suggest that relatively reduced inhibition of the left hemisphere by the right – which manifests in greater left than right-frontal asymmetry – may be involved in impulsive behavior.

Relationships with Hormonal Responses and Other Physiological Responses

Recent research suggests that frontal activity also mediates a hormonal response to stressful events. The steroid hormone cortisol is instrumental in the generation of withdrawal and avoidance responses to stressful situations and potential threats. Consistent with research identifying the motivational aspects of the frontal cortex, salivary cortisol increases following a battery of stress inducing tasks (e.g., cold presser, speech, difficult mental arithmetic) were correlated with frontal activity. Specifically, cortisol increases were negatively correlated with asymmetry metrics, such that higher cortisol levels were observed in individuals with greater rightward asymmetry (Quaedflieg, Meyer, Smulders, & Smeets, 2015). Frontal asymmetry has also been related to the amplitude of event-related potentials (ERP) that occur in response to aversive, negative events such as errors. Several studies have reported that front left cortical activity at rest is inversely correlated with amplitude of the Error-Related Negativity (ERN). The ERN is typically observed following self-performed errors, is thought to reflect the monitoring of and sensitivity to negative events. In both the Stroop Task and the Multi-Source Interference Task, Nash, Inzlicht, and McGregor (2012) found that leftward asymmetries at rest were correlated with smaller ERN amplitudes and rightward asymmetries were correlated with larger ERN amplitude.

Recent work examining the role of cortical asymmetries in predicting empathic responses provides initial evidence that the disinhibition of withdrawal-related frontal circuity can be involved in the promotion of pro-social empathic behavior. Tullett, Harmon-Jones, and Inzlicht (2012), for instance, found that greater right-frontal activity was associated with greater levels of empathic concern toward disadvantaged children presented in a picture viewing task. This effect was statistically mediated by self-reported sadness, such that the increased sadness predicted increased levels of empathic concern. Importantly, however, frontal activity was not associated with self-reported *intention* to volunteer with organizations involved in alleviating the suffering depicted in the picture stimuli, suggesting that although right-frontal activity may be important for engendering sadness-derived pro-social affects such as empathy, this does not necessary transfer to approach-related intentions to help.

Alpha asymmetry has also been related to a diverse range of other affective and motivational variables. In particular, a number of studies have found that asymmetrical frontal cortical activity is related to the functioning of behavioral inhibition (BIS) and behavioral approach (BAS) systems. BIS and BAS have been proposed as fundamental neural systems underlying the generation and maintenance of behaviors that are instrumental in threat avoidance (BIS) and appetitive behaviors (BAS; Gray & McNaughton, 2003). Using self-report scales developed to capture the functioning of these systems (Carver & White, 1994), Harmon-Jones and Allen (1997) observed that left-frontal activity was positivity correlated with scores on the BAS scale but asymmetrical frontal cortical activity was unrelated with scores on the BIS scale (also see, Quaedflieg et al., 2015; Sutton & Davidson, 1997). Other studies have found that BAS scores are correlated with greater relative left-frontal activity and that BIS scores are correlated with greater relative right-frontal activity (Sutton & Davidson, 1997). Consistent with the results of Harmon-Jones and Allen (1997), Coan and Allen (2003) found that BAS scores were positively correlated with left-frontal activity, but that BIS scores were *not* positively correlated with right-frontal activity (also see, De Pascalis, Cozzuto, Caprara, & Alessandri, 2013). At present, no research has identified why BIS is related inconsistently with right-frontal cortical activity. It is possible that the inconsistency in results is due to the complexity of the persons scoring high in BIS; some may chronically use approach-related rather than avoidance-related strategies to address their sensitivity to threats and punishments.

Several recent studies have examined the relationship between frontal cortical activity and specific forms of approach-related behavior. For instance, greater left-frontal activity has been positively correlated with self-reported sensation seeking and risk taking in adults (Santesso et al., 2008). Recent work has also shown that amount of effort individuals take to obtain rewards is correlated with alpha asymmetry. Hughes, Yates, Morton, and Smillie (2014) examined choices in the Effort Expenditure for Rewards Task (EEfRT). In the EEfRT, participants are asked to decide between trials which may result in small rewards, but are easy, and trials that may result in large rewards, but require more effort to complete. On each trial, participants are also informed of the probability that they will receive a reward at the end of the trial. Interestingly, left-frontal cortical activity predicted the proportion of hard trials that participants selected regardless of the probable outcome, as well as their tendency to select a higher proportion of hard trials even when there was a low chance of receiving a reward (Hughes et al., 2014).

WHAT IS BEING MEASURED DURING A RESTING BASELINE SESSION?

The early studies seemed to be based on the assumption that the brain activity measured during a baseline resting session was relatively fixed and tapped a trait-like variable. Given the number of studies that have found baseline resting brain activity to relate to trait emotive variables, this assumption seems correct. However, some of the early research suggested that this baseline resting brain activity may not be fixed or stable and some studies recorded participants' brain activity at two different sessions separated by a few weeks or months. These studies revealed that the baseline resting brain activity was more likely to relate to other measures of emotive traits for individuals who showed similar patterns of brain activity across two separate sessions (Tomarken, Davidson, Wheeler, & Kinney, 1992). Later research recorded baseline resting brain activity from the same individuals for four sessions, each separated by several weeks (Hagemann, Naumann, Thayer, & Bartussek, 2002). Results from this important study revealed that roughly half of the variance in asymmetrical frontal cortical activity was due to trait influences but the other half of the variance was due to state influences.

Frontal asymmetry has also been found to have relationships with situational and environmental variables that are unavoidable in any context, specifically, time of day and time of year. Variation in frontal alpha asymmetry – and corresponding shifts in approach or withdrawal motivation, respectively – at different times of the day, and different times of the year, may contribute to differences in the manifestation of adaptive or maladaptive behaviors in students. Initial evidence for a relationship between time of day and time of year and alpha asymmetry was provided by studies examining circadian and seasonal effects on cortisol levels. Cortisol is a steroid hormone that is most commonly associated with stress-related responses (Bertsch, Böhnke, Kruk, Richter, & Naumann, 2011; Virkkunen, 1985). In humans, cortisol levels peak following waking and gradually decrease throughout the day. Cortisol levels also fluctuate through the year, and are lowest during spring and highest during fall and winter (Walker, Best, Noon, Watt, & Webb, 1997). Importantly, these circadian and seasonal variations in cortisol levels have been found to correspond to differences in affective and motivational behaviors. For instance, individuals moods tend to be more negative early in the day and become increasingly positive as time goes on (Wirz-Justice, 2005), while depression and anhedonia is most frequent during fall and winter months than during spring months (Nayyar & Cochrane, 1996).

Fluctuations in cortisol levels have also been found to be related to differences in frontal alpha asymmetry. For instance, a bolus of intravenously administered cortisol increases relative rightward asymmetry (Tops et al., 2005), as does the oral administration of a cortisol pill (Tops, van Peer, Wester, Wijers, & Korf, 2006), and cortisol levels in infants is correlated with both increased rightward frontal asymmetry and withdrawal behaviors (Buss et al., 2003). Taken together, the seasonal variations in cortisol, affective motivation, and the manipulation of alpha via cortisol administration suggest a potential link between circadian and seasonal mood states and frontal alpha asymmetry. If this is the case the variation in recording parameters such as time of day and time of year may yield variation in alpha asymmetry. This hypothesis was initially tested by recording EEG at different times of the day and different seasons across a large sample of participants. While overall differences in frontal asymmetry were not observed as a function of time of day, there was an interaction between time of day and season of recording, such that the greatest rightward asymmetry was observed in participants whose data were recorded during fall mornings (Peterson & Harmon-Jones, 2009). Note that subsequent studies have had difficulty in consistently replicating this effect, with frontal asymmetry not varying as a function of the interaction between recording time and season (Velo, Stewart, Hasler, Towers, & Allen, 2012).

STATE RELATIONSHIPS WITH MOTIVATION

The research discussed above provides evidence for the role of asymmetrical frontal cortical activity as a mediator and moderator of motivational processes. However, despite the diversity of this research, it is inherently limited by its correlational nature, and thus only provides partial evidence for the role of cortical asymmetries in motivation. This limitation has been addressed by the use of an experimental approach to frontal activity, providing convergent evidence of the findings reported in the correlational literature, and clarifying the particular conditions where the approach versus withdrawal conceptualization of frontal asymmetry is most consistently observed: when the elicitation context is meaningful for the individual, such as in response to highly desired stimuli.

These experimental studies fall into two broad classes. First, there are experimental studies that manipulate approach and/or withdrawal states and subsequently examine the effect that these manipulations have had on frontal cortical activity. Second, there are experimental studies that directly or indirectly manipulate neural activity in the frontal cortex, and examine the effect that these manipulations have had on behavior and other physiological indices.

Manipulation of Motivational State

Hemispheric differences in the activation of the frontal cortex during motivational and affective events have been observed in a range of contexts, including relatively simple picture viewing (Gable & Harmon-Jones, 2008), through to emotions such as reactive aggression that are generated by social interaction (Harmon-Jones & Sigelman, 2001). These differences in activation emerge early in development, with greater left-frontal activity when viewing approach-related stimuli (e.g., happy faces), and greater right-frontal activity when viewing withdrawal-related stimuli (e.g., sad faces) being initially observed in 10-month old infants (Davidson & Fox, 1982). Similar patterns were also observed using one of the most basic, and cross species, methods of evoking pleasant or unpleasant experiences – taste. In this study, researchers administered small amounts of water, citric acid, and sucrose to 10-month old infants while EEG was recorded. Consistent with the emerging data regarding the distinct emotional and motivational functions of the left and right-frontal cortices, the administration of sucrose was associated with greater left than right-frontal activity than the administration of water or citric acid (Fox & Davidson, 1986). These patterns of activation have been reported in adults, with greater left fontal activity when participants viewed film clips that evoked feelings of happiness than when they viewed film clips that evoked feelings of disgust. Moreover, these differences were greater during the actual *expression* of these approach and withdrawal-related emotions, suggesting that lateralized frontal activation is instrumental in the generation and expression of motivational responses (Davidson, Ekman, Saron, Senulis, & Friesen, 1990).

There is also direct evidence that lateralized brain activity occurs specifically in response to and during approach-related states. For instance, when preparing to act in the pursuit of a small monetary reward, greater left-frontal than right-frontal activation has been observed (Sobotka, Davidson, & Senulis, 1992). More recent work has observed a positive correlation between the amplitude of the frontal-late positive potential (f-LPP) and frontal asymmetry during stimuli viewing (Poole & Gable, 2014), suggesting that frontal activation is implicated in allocation of attention toward motivationally important features of the environment. Several studies have shown that when measured over the left-frontal cortex, the f-LPP is preferentially sensitive to approach-related stimuli, such as images that evoke desire, an effect that is not observed when the f-LPP is measured over the right-frontal cortex (Gable & Harmon-Jones, 2010). Similar findings have also been observed with respect to the modulation of frontal asymmetry by the presentation of highly desired images: in individuals who find dessert foods to be highly appetitive, enhanced left-frontal activation is observed during viewing of cake and dessert photos, while this effect is not observed in individuals who do not find dessert food to be highly appetitive (Gable & Harmon-Jones, 2008).

Several studies have provided evidence that increased left-frontal activity occurs in response to provocative events. For instance, individuals who are subjected to experimentally manipulated social ostracism show increased levels of left-frontal activation (Peterson, Gravens, & Harmon-Jones, 2011). Moreover, the increase in anger-related left-frontal activation is associated with behavioral aggression (Harmon-Jones & Sigelman, 2001; Verona, Sadeh, & Curtin, 2009).

Additional evidence for a causal role of asymmetrical frontal activity also comes from studies examining different subtypes of empathic behavior. In young children (6–10 years of age), increased right-frontal activity during a positive mood induction has been found to predict greater empathic cheerfulness (i.e., the expression of positive affect in response to the expression of negative affect in another person), while increased left-frontal activity predicts greater expression of empathic happiness (i.e., the experience of positive affect when exposed to it in another; Light et al., 2009).

Manipulation of Cortical State

Hand Contractions

Interestingly, motivational state and the underlying cortical asymmetry are amenable to manipulation by surprisingly simple behaviors. In particular, alterations in the movement of facial and hand muscles on one side of the face or body are sufficient to alter the emotional and motivational behaviors that appear to be underpinned by the contra-lateral hemisphere. Because afferent and efferent feedback are projected from and to the contra-lateral hemisphere, the asymmetrical innervation of these muscles can manipulate emotional and motivational experiences. For instance, contractions of the left side of the face and left-hand have been found to increase feelings of withdrawal-related emotions such as sadness, while contractions of the right side of the face and right-hand have been found to increase indirect measures of approach motivation, such as perseverance (Schiff, Guirguis, Kenwood, & Herman, 1998; Schiff & Lamon, 1989, 1994). These data suggest that right-hand contractions might enhance approach motivation, while left-hand contractions might enhance withdrawal motivation. If so, alterations in frontal alpha asymmetry should also be observed, consistent with its role in motivational direction and intensity.

A series of studies have since tested this hypothesis, and examined the extent to which the earlier effects on emotional and motivational experience might be underpinned by changes in frontal asymmetry. In the first of these, Harmon-Jones (2006) had participant spent a total of 90 seconds contracting their left- or right-hand around a small rubber ball. Following these contractions, participants listened to a mildly positive, approach-related audio recording, EEG was recorded, and finally participants completed a brief emotional state questionnaire (Watson, Clark, & Tellegan, 1988). Three key effects were observed. First, contra-lateral hand contractions were associated with greater cortical activity on the contra-lateral hemisphere (e.g., reduced alpha power). Second, participants contracted their right-hand had higher levels of positive affect than participants in the left-hand condition. Finally, and most importantly, the participants in the right-hand-contraction condition had greater leftward asymmetry than participants in the left-hand condition.

Two successive studies have since found that the manipulation of frontal cortical activation by hand contractions can also influence motivational experiences in relatively complex social situations. For instance, Peterson, Shackman, and Harmon-Jones (2008) found that contra-lateral contractions contribute to changes in frontal asymmetry and aggression toward other persons. Specifically, participants engaged in more reactive aggression to a person who had insulted them if they had performed right-hand contractions than if they had performed left-hand contractions. Similarly, right-hand contractions also influence aggressive response to ostracism (Study 2, Peterson et al., 2011). Replicating the results of previous studies (Harmon-Jones et al., 2010; Peterson et al., 2008) relatively greater left-frontal activity was observed following right-hand contractions than left-hand contractions. Importantly, the increases in left-frontal activity observed in participants who contracted their right-hand were also associated with increased feelings of ostracism and anger, consistent with the approach motivation conceptualization of frontal cortical activity.

Transcranial Direct Current Stimulation (tDCS)

Frontal asymmetry and motivational behavior can also be manipulated via the application of low intensity electrical current to the scalp. This method, tDCS, has been found to increase cortical excitability and activity, with enhancement observed for up to an hour following an initial 10-minute tDCS application (Nitsche et al., 2008).

Several studies have since taken advantage of the insights that tDCS-based methods can provide. Mirroring the findings of the hand-contraction studies reviewed above (Harmon-Jones et al., 2010; Study 2, Peterson et al., 2008, 2011) the application of tDCS to the left hemisphere has been found to increase reactive aggression following insulting feedback, while tDCS to the right hemisphere did not (Hortensius, Schutter, & Harmon-Jones, 2012). Moreover, self-reported anger in response to the insulting feedback predicted the intensity of aggressive behaviors directed toward the person who insulted them, but only for participants who received left-frontal tDCS. tDCS has also been observed to affect other types of aggression. While the studies discussed above utilize reactive aggression tasks (e.g., aggression as a physically or socially defensive action), aggression can also be proactive (e.g., unprovoked, or used in pursuit of a goal). In a recent study, proactive aggression was lower in male participants who received sustained tDCS to the *right*-frontal hemisphere, but not in female participants, or male participants who received sham tDCS stimulation (Dambacher et al., 2015). That is, the relative enhancement of right hemispheric activity was found to reduce approach behavior – potentially via the enhancement of withdrawal-related motivation instantiated by the right-frontal cortex.

Other studies have applied the tDCS methodology to other emotions that may have approach-related aspects, such as jealousy. Jealousy occurs in response to perceived or real threats to dyadic relationships by a third party. These relationships need not be current, and jealousy can occur in response to perceived threats to a relationship between an individual and someone that they desire. Despite jealousy being an unpleasant emotional experience, much like the conceptually similar emotion of anger, it has distinct approach-related aspects. Moreover, the experience of jealousy can be manipulated via the application of tDCS. In a recent study, Kelley, Eastwick, Harmon-Jones, and Schmeichel (2015) examined the effect of left-frontal, right-frontal or sham tDCS on self-reported jealousy in participants who were either included or excluded from interacting with a desired partner by a same-sex competitor in a modified ostracism task. Unsurprisingly, participants who were excluded expressed greater jealousy than those who were included. Moreover, greater jealousy was reported by participants who received left-frontal tDCS than those who had received right-frontal or sham.

Other

The alteration of frontal alpha asymmetry can also occur through pharmacological manipulations, such as Tryptophan depletion (TD). Tryptophan (TRP) is a precursor in the synthesis of serotonin (5-HT; Zhang, Beaulieu, Sotnikova, Gainetdinov, & Caron, 2004), and the administration of acute TD (ATD) compounds significantly decreases the levels of TRP and 5-HT in humans and rodents (Carpenter et al., 1998; Moja, Cipolla, Castoldi, & Tofanetti, 1989; Moore et al., 2000). ATD has been found to cause short-term and reversible depressive responses in individuals with a personal history of depression (Moreno, Heninger, McGahuey, & Delgado, 2000), and those at risk of developing depression (Benkelfat, Ellenbogen, Dean, Palmour, & Young, 1994), although there is considerable variability in the extent to which these symptoms are present. Because of the link between depressive symptoms reported in correlational studies (discussed in the previous sections), Allen, McKnight, Moreno, Demaree, and Delgado (2009) predicated that greater right-frontal asymmetry following TD may also be observed, and may predict the experience of depressive symptoms in subsequent months. Interestingly, and contrary to prevailing theories of frontal asymmetry, greater rightward asymmetry following ATD predicted a *reduced* likelihood of depressive symptoms in the following six months, a finding that seems at odds with the conceptualization of enhanced rightward asymmetry as reflecting enhanced withdrawal motivation. Because participants who presented smaller rightward asymmetry following ATD were more likely to develop depression, Allen et al. (2009) suggested that a relative inflexibility of asymmetry responses is greater predictor of vulnerability to depression. If true, this interpretation suggests that the more simplistic viewpoint that a general hyperactive rightward response to ATD – or other events that provoke a depressive response – is insufficient, and consequently creates an inaccurate characterization of how frontal asymmetry relates to depression risk factors.

PARIETAL ASYMMETRY AND PARIETAL-FRONTAL INTERACTIONS

Recent research suggests that asymmetrical activity over the parietal cortex and the interaction between frontal and parietal regions may also be important for the instantiation of behaviors with varying motivational direction and intensity. Although research examining the precise relationship between frontal and parietal asymmetries is presently limited, there is converging evidence that the interactions between these regions may be important mechanism for the instantiation of approach- and withdrawal-motivated associated behaviors associated with frontal asymmetry.

The frontoparietal literature has developed in parallel to the frontal asymmetry literature, and has typically focused on connectivity between frontal and posterior regions of cerebral cortex and their relationship to cognitive processes such as memory and attention (Babiloni et al., 2004; Lee et al., 2009; Sabatinelli et al., 2014; Staines, Padilla, & Knight, 2002). Importantly, combined functional magnetic resonance imaging (fMRI) and EEG data has shown that alpha power is inversely related to the ongoing functioning of this network (Mantini, Perrucci, Gratta, Romani, & Corbetta, 2007). In the

EEG, connectivity within this network is commonly assessed using the coherence between alpha power measured over frontal and parietal regions (Lee et al., 2009).

Frontoparietal connectivity has been implicated in a diverse range of cognitive functions that are integral to the implementation of approach and withdrawal motivational behaviors (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). For instance, several studies within the animal literature have shown that enhanced frontoparietal connectivity in the alpha band is observed under conditions that require increased use of working memory (Salazar, Dotson, Bressler, & Gray, 2012), as well as the preceding the initiation of controlled movements (Phillips, Vinck, Everling, & Womelsdorf, 2014). In humans, frontoparietal connectivity has been associated with spatial attention (Capotosto, Babiloni, Romani, & Corbetta, 2009), with repetitive transcranial magnetic stimulation (rTMS) to regions of the frontal cortex reducing parietal and occipital alpha power, and drastically reducing visual attention performance (Capotosto et al., 2009). Frontoparietal connectivity has also been implicated in the preparation of attention and motor intentions, with reciprocal feedback between the frontal and parietal regions occurring prior to the voluntary direction of attention to a specific location and or preparation to make a voluntary behavioral response (Praamstra, Boutsen, & Humphreys, 2005).

The link between frontoparietal connectivity – particularly in the alpha band – and attentional and behavioral control has led to the suggestion frontoparietal network function may be one mechanism by which asymmetrical frontal activity affects motivated behaviors. Grimshaw and Carmel (2014) suggest that the frontal cortices engage in executive control over other aspects of the frontoparietal network such as the posterior parietal cortex, with the right hemisphere inhibiting approach-related processes, and the left hemisphere inhibiting withdrawal-related processes. While the above studies suggest that parietal asymmetries and interactions with frontal asymmetry may be related to motivational intensity and direction, direct evidence for this is mixed. In general, studies have found that parietal asymmetries at rest either do not predict motivational intensity and direction, or that partial asymmetries are not affected by variables that manipulate motivational state (Peterson & Harmon-Jones, 2009). More commonly, the measurement of parietal activity serves to highlight the exclusive contribution of frontal activity to motivation-related outcomes.

Nevertheless, several studies have found that parietal asymmetries, and interactions between sites implicated in the frontoparietal network can predict divergent approach and withdrawal behaviors. For instance, while

Tullett et al. (2012) found that right-frontal asymmetry predicted increased empathic feelings, they also found that right parietal asymmetry was also associated with increased empathy. Frontoparietal effects on motivational behavior have also been reported with respect to attentional processes involved in emotional face perception. The allocation of attention to faces with angry facial expressions can be vigilant – attention is sustained toward a potential threat or challenge, or avoidance – attention is forcefully directed away from a potential threat. A recent study that investigated the extent to which frontal and parietal asymmetries predict these behaviorally distinct forms of attention allocation reported that while resting frontal asymmetry alone did not predict the strength or direction of these attentional biases, an interaction between frontal and parietal asymmetry did. Specifically, in participants with right-frontal asymmetry, leftward parietal asymmetry predicted increased vigilance toward angry faces, while rightward parietal asymmetry predicted increased avoidance of angry faces (Grimshaw, Foster, & Corballis, 2014).

CONCLUDING REMARKS

Extensive research conducted over the past 30 years has provided evidence that hemispheric asymmetries in electrocortical activity are functionally important for motivational processes. While frontal asymmetries are associated with a diverse range of processes, from responses to rewarding stimuli to neural activity related to errors, these processes generally cluster into those involved in approach and those involved in withdrawal. Specifically, relative leftward asymmetries are associated with approach motivation-related behaviors, while relative rightward asymmetries are associated with withdrawal motivation-related behaviors. These relationships are bidirectional, such that resting asymmetries predict approach and withdrawal behaviors, and exposure to situations that produce approach or withdrawal motivation yield changes in frontal asymmetry.

However, the mechanism by which asymmetrical frontal activity produces alterations in attention, memory, and other constructs related to motivational direction and intensity is unclear. While a small literature suggests that connectivity between frontal regions that appear to underlie motivational processes and more parietal regions that underlie the outwards manifestations of motivated actions may be important, findings have been generally inconclusive. Identifying the precise mechanism by which frontal asymmetry acts on motivational processes may be difficult to achieve, given the intrinsic complexity of the systems that are likely to be involved. Nevertheless, doing so will be central to developing an improved understanding of how networks within the brain coordinate to produce behaviors that allow for approach and withdrawal.

NOTE

1. This conceptualization of interacting but independent processes has previously been applied to the constructs of positive and negative affect (Diener & Iran-Nejad, 1986). The simultaneous experience of pleasant and unpleasant affect is most likely to occur when at low levels of intensity and arousal. At higher levels of intensity, the affect experienced is largely positive *or* negative, giving the appearance of a bipolar continuum.

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NEUROSCIENCE OF MOTIVATION AND ORGANIZATIONAL BEHAVIOR: PUTTING THE REINFORCEMENT SENSITIVITY THEORY (RST) TO WORK

Philip J. Corr, Neil McNaughton,
Margaret R. Wilson, Ann Hutchison,
Giles Burch and Arthur Poropat

ABSTRACT

Neuroscience research on human motivation in the workplace is still in its infancy. There is a large industrial and organizational (IO) psychology literature containing numerous theories of motivation, relating to prosocial and productive, and, less so, "darker" antisocial and counterproductive, behaviors. However, the development of a viable over-arching theoretical framework has proved elusive. In this chapter, we argue that basic neuropsychological systems related to approach, avoidance, and their conflict, may provide such a framework, one which we discuss in terms of the Reinforcement Sensitivity Theory (RST) of personality.

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We argue that workplace behaviors may be understood by reference to the motivational types that are formed from the combination of basic approach, avoidance, and conflict-related personalities. We offer suggestions for future research to explore workplace behaviors in terms of the wider literature on the neuroscience of motivation.

Keywords: Motivation; personality; RST; reinforcement sensitivity theory

Human motivation in the workplace has been a central theme in industrial and organizational (IO) psychology for, at least, the last one hundred years. This literature contains numerous theories that are used routinely to provide explanations for the systematic patterns of behavior observed – both prosocial/productive, and "darker" antisocial/counter-productive ones (Koopmans et al., 2011). As we shall see, motivation can be exerted in different directions and not always to meet organizational objectives. We are all familiar with "empty labor" (Paulsen, 2014) – organizational "misbehavior," that is, time spent in private activities (e.g., surfing the web, chatting on social media, and talking to colleagues on non-work-related matters) during paid working hours – and there is the darker side to organizational behavior in the form of bullying and back-stabbing (Furnham, 2015), and also "empire building". All impair organizational effectiveness, and the subjective well-being of employees.

What has been missing in this important applied literature is consideration of the neuroscience of workplace motivation. In this chapter, we attempt to fill this lacuna by showing how motivational types are formed from the combination of basic approach, avoidance, and conflict-related personalities. Although there is now much known about the basic neuroscience of these processes, there has been a reluctance to extend this knowledge to workplace motivation and behavior – this is largely the result of the traditional separation of these two fields of psychology. As authors who are variously specialized in basic neuroscience, motivation and personality psychology, occupational/organizational behavior, and clinical psychology, we are well-placed to tie together these hitherto disparate areas of research.

Motivational factors are clearly important contributors to individual and organizational performance. Much has been learnt during the past few decades about how contextual factors affect work performance, especially with respect to managerial interventions (Steel & König, 2006) and social influences (Colquitt et al., 2013; Loi, Chan, & Lam, 2014). However, organizations and researchers have also been very interested in individual differences and their contributions to work performance, especially the role played by personality. Such has been the volume of research in this area that Barrick, Mount, and Judge (2001) called for a moratorium on empirical reviews of personality and performance, suggesting instead that researchers should focus on exploring explanations of the role of personality at work.

Unfortunately, the dominant model of personality assessment used in organizational research, the Big Five or Five-Factor Model (FFM), has restricted usefulness for explanatory purposes due to its largely atheoretical foundation (Poropat & Corr, 2015). For this reason, the aim of this chapter is to review the explanatory value of a general theory of personality-related human motivation derived from the wider neuroscience literature. We argue that this model may have the potential to split the general motivational work "drive" atom of individual employees into its constituent neuropsychological parts.

WORKPLACE INITIATIVES AND MOTIVATION

Developments in IO psychology theory have led to a reasonable understanding of how to motivate employees – through various initiatives, such as job design, incentive structure, well-being interventions, and objective-setting (Arnold et al., 2010). Despite early psychoanalytical interpretation of the unconscious motives of employees (Argyle, 1973), most organizational interventions are based on the bedrock of neo-classical economic assumptions, namely, behavior is "rational" – although, in individual cases, subject to constraints – and individuals are assumed to seek utility optimization reflecting their non-biased processing of information in the environment guided by a consistent set of preferences. According to this view, a change in, for example, incentives should shift the behavior of the rational agent (*homo economicus*) in the desired direction. Social exchange theory provides an example: employees are assumed to match their effort and contribution to the support provided by their employers and managers (Colquitt et al., 2013). In this way, IO behavior is seen to be flexible and responsive to initiatives designed to harmonize with organizational objectives. As a big-picture theory, there is much to commend this approach especially as applied to the *aggregate* behavior of groups.

Despite its notable virtues, this perspective singly side-steps two major problems. The first is the prevalence and significance of individual variations in how people react to initiatives, how they process information, and their specific preference structures in relation to work. For example, what counts as intrinsic or extrinsic factors of motivation, such as self-worth versus financial remuneration, depends on the individual rather than their context (Deci & Ryan, 2000). The second problem relates to evidence that, although behavior may be flexible, its underlying motivational structure and dynamics are not. According to this perspective, behavior is the *product* of personality characteristics (e.g., traits such as achievement striving, which are relatively stable) as well as situational factors (e.g., opportunities for advancement, which are not stable). The growing wealth of research demonstrating personality factors have greater influence on work and life outcomes than do social circumstances (Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007) attests that personality-linked differences in motivation are crucial for understanding work performance.

Ignoring individual differences in reactions to workplace initiatives demands excessive faith in the power of the behaviorist black-box approach which permits no causal role for pre-existing motivational dispositions. From that approach, where individual differences are seen to exist, they are the result of the selective shaping by a history of schedules of reinforcement, and with enough effort can be unshaped by different schedules. Whatever the truth in this belief, the neuroscience of motivation, and its related emotion and personality processes, suggests strongly that this approach has, at the very least, marked limitations. For reinforcement to work it must go through the brain and we know that there exist considerable individual differences in neural processing (Corr & McNaughton, 2012). In the workplace, as well as life more generally, people are motivated in different ways and to different extents (Nicholson, 2000). The previously cited research of Roberts et al. (2007) provides ample evidence that, at the higher level of omnibus general "drive," there is considerable variation, which is expressed in individual outcomes such as work performance and achievement.

In this chapter, we argue that the one-size-fits-all approach to understanding motivation in the workplace is not appropriate to account for observed realities, especially regarding the significant differences between people in personality, attitudes, and aspirations. We argue that general constructs, such as "drive," need to be broken down to their components parts in order to get a better grip of the underlying motivational dynamics of workplace behavior. To achieve this end, we rely upon the extant literature on the neuroscience of motivation and personality – to consider the former necessarily entails the latter.

MOTIVATION, DRIVE, AND PERFORMANCE

Organizations of all kinds need top-performing employees in order to gain the best outcomes for clients, customers, owners, and so on. Among individual differences variables, cognitive ability is typically the strongest predictor of employee performance (Schmidt & Hunter, 1998), but personality has repeatedly been shown to be reliably associated with a wide range of job-related behaviors (Barrick & Mount, 1991; Burch & Anderson, 2008a, 2008b; Hurtz & Donovan, 2000).

The confirmation of the role of personality at work helped researchers address a long-standing gap in methods of assessing employees. Specifically, it has long been accepted that performance is a function of ability, motivation, and opportunity (Blumberg & Pringle, 1982). Ability is generally linked to intelligence and prior learning (training, experience, and education), while opportunity is dependent upon resources such as time, money, and equipment. These factors effectively represent the "can do" aspect of performance, whereas the "will do" aspect has often been investigated by considering contextual factors such as leadership and goal-setting interventions (Locke & Latham, 2002). The recognition of the role of personality in work performance has demonstrated that the "will do," or motivation component of performance, is also reliably associated with systematic individual differences.

Thus, researchers and practitioners need to both acknowledge and understand the role of personality in workplace motivation. Although all of the previously cited reviews of personality in the workplace used the FFM to organize their analyzes, this descriptive model of personality provides little guidance with respect to explaining how personality relates to motivation. To achieve adequate explanation, it is necessary to identify how stable and persistent individual differences in neuropsychological systems mediate behavioral reactions to workplace stimuli, such as the typically complex compounds such as managerial "instructions" and "initiatives" to which employees need to respond.

An important assumption of our approach is that, at the level of the individual, behavioral reactions cannot be just "read-off" from what is already known, or more usually assumed to be known, about the average effects of such motivating stimuli. An example of this would be that the implementation of performance-management procedures might be rewarding for one person, but insulting to another. In thinking about these matters, we should remember Kluckhohn and Murray's (1950, p. 190) statement, "every man is in certain respects: (a) like all other men, (b) like some other men, and (c) like no other man." In this specific and other respects, personality differences are important because they reflect deeper motivational processes that drive behavior – indeed, as elaborated below, personality traits are often the collective expression of these subsets of processes.

Our claim is that people have a specific biological make-up: significant variation exists in the operating parameters of neuropsychological systems that result in specific levels of different forms of emotion and motivation that, in combination, produce what is observed in the workplace as general "drive" (Furnham, 1992). In addition, any viable explanation of motivation should consider, at the very least, three outcome components: (1) intensity; (2) direction; and (3) persistence of effort (Latham, 2007), or "sustainability." It is this higher order construct of drive that is proximally related to performance, both in terms of quality and quantity, and psychological sustainability. As such, drive can be related to resistance to disruption and frustration, and can be predicted by consideration of its component parts (e.g., a burst of creative high drive to initiate a new project may either be sustained by the reinforcement of intermediate steps of success or inhibited by frustration entailed during early planning stages).

Within this context, drive is a nonspecific general factor of motivation (rather like the concept of general arousal), and can influence both productive and counter-productive behaviors. In this sense, "drive" reflects the urge to express basic needs, composed of biological imperatives (e.g., social utility achieved through influence, affiliation, achievement, and reputation; and, avoidance of social loss through "face saving," control, and manipulation). A high level of drive can benefit or harm the organization, depending upon the alignment of individuals' and organizations' goals.

In putting forward these arguments, we are taking a *dispositional* approach to motivation. Although there are links between personality and motivation (Judge & Ilies, 2002), and attempts have been made to develop dispositional theories of employee motivation, there is no over-arching framework to explain why some people are more motivated than others, and in different ways. We agree with Locke (1991, p. 288): There is a "plethora of theories and paucity of frameworks." We believe that the challenge lies in the (structural) complexity of motivation as a construct.

ATTRACTORS AND REPULSORS IN THE WORKPLACE

The approach we outline is based on several tenets. Firstly, emotions (e.g., fear and hope) are central states activated by reinforcing stimuli (generally called "punishment" and "reward" but in the workplace commonly referred to as "discipline" and "incentives"); and, secondly, two major neuropsychological systems underpin the activation of these central states, one related to sensitivity/reactivity to "punishment" and another to "reward." We set these terms in quotes because they are in need of delineation and clarification, which we provide below. We also assume that, at least in part, individual differences, as expressed in personality traits (e.g., extraversion and neuroticism), reflect long-term stabilities in the operation of these state systems (for discussion of these relations, see Corr, DeYoung, & McNaughton, 2013).

Before developing this argument further, we note that there are a limited number of degrees of freedom of behavioral reactions, at least at the low level of explanation we explore in this chapter. Whether a simple stimulus or complex organizational initiative, there are three possible forms: (a) avoidance, (b) approach, or (c) decision-behavior equivocation. In an important sense, all forms of behavior, which at the surface level can be complex and multifaceted, reduce to these three behavioral degrees of freedom. This conceptual simplicity should not be read as implying that they cannot account for the panoply of complex behaviors seen in the workplace. In much the same way that the operation of only three types of cones in the retina, which are maximally sensitive to different wavelengths of light, lead to the experience of a seemingly countless number of colors, so too with (relatively) simple neuropsychological systems and organizational behavior.

Attractors and Repulsors as "Reward" and "Punishment"

In the most general terms, "reward" stimuli motivate approach behavior *toward* some desired end state, and "punishment" stimuli motivate avoidance/escape behavior *away* from some undesired end state (Gray, 1975). It is important at this point to define these operations in terms of the *perception* of the reacting individual and not what the experimenter, or manager, believes they are providing. Consequently, *evaluation* of stimuli is the first step to something being categorized as "rewarding" or "punishing" (to avoid these ambiguous terms, we prefer to label them "attractors" and "repulsors," respectively; Corr & McNaughton, 2012): Attractors cue positive-approach behaviors; repulsors cue negative-avoidance behaviors. In this context, "negative-avoidance" is not necessarily undesirable – the outcome may be productive, such as not wasting further time on frustrating and, ultimately, non-productive tasks or people. The central role of perception in this understanding of cued behaviors leads to a performance-management problem because the same stimulus may be an attractor for one person, but a repulsor for another person, or ignored by a third person. In other words, motivational significance is not contained in the stimulus, but in the person's *reaction* to the stimulus.

In terms of attractors and repulsors, a number of complexities need to be faced. At the moment-to-moment state level, attractors and repulsors produce approach and avoidance motivational tendencies, respectively. However, attractors and repulsors subtract from each other to produce the final net product of motivation, and have different goal-gradients. Specifically, the gradient for repulsors is steeper than that for attractors. Mathematically formulated in Neil Miller's analysis of approach-avoidance conflict in the rat, much earlier Darwin had noted that we value blame much higher than praise. A parallel notion is now fashionable in behavioral economics in the concept of loss aversion, in which losses loom (by a factor of 2) larger than gains (Kahneman, 2012), especially when the potential loss is made salient. In psychology, bad feedback, emotions and news almost always outweigh the good (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001). We dislike being criticized much more than we like being exalted, and this is an important factor of motivation in the workplace given the central role of feedback in contributing to performance (Kluger & DeNisi, 1996).

In addition to these two attractor and repulsor systems, there is another system of "avoidance": Over and above these subtractive effects, the (passive) *inhibition* and avoidance by approach-avoidance *conflict* is neurally and psychopharmacologically distinct from simple (active) avoidance (Gray, 1982; Gray & McNaughton, 2000): Although avoidance and inhibition can look very alike, their functional roles are quite different.

These subtractive and inhibitory effects provide the major theoretical rationale for assuming combined effects of motivationally salient stimuli in the workplace. They do add complexity, but also realism and theoretical, and it is to be expected practical, heft. This perspective draws attention to the motivational complexity of most workplace situations, and the theoretical challenges that confront any attempt to account for them.

The general form of our argument is consistent with trends in recent years to apply fundamental neuroscience ideas to human behavior in different spheres, for example, the neuroscience of economic decision-making (i.e., neuroeconomics; e.g., Politser, 2008). Here, we extend neuroscience ideas, specifically those related to motivation and emotion, to industrial-organizational (IO) motivation and behavior.

REINFORCEMENT SENSITIVITY THEORY (RST) AND DRIVE

A person's dispositional level of "drive" – as the super-ordinate construct that has received most attention in the IO literature – is an important determinant of type and level of performance in the workplace. The component parts of this drive may be explained by the *reinforcement sensitivity theory* (RST), which is a neuroscientific theory of motivation, emotion and learning, extended to personality psychology, by the neuropsychologist Gray (1982) and later developed by colleagues (Corr & McNaughton, 2012; Gray & McNaughton, 2000, McNaughton & Corr, 2004, 2008) – this is summarized in a collective work edited by Corr (2008a). RST seeks to provide an explanatory dispositional framework that is lacking in IO motivational research, allowing the combination of theories of workplace motivation with neuroscience. We present a few selected findings and arguments that demonstrate the potential RST holds for providing a holistic, dispositional explanation of workplace motivation.

Although other models of personality have seen greater use in organizational settings, they have typically been based on the atheoretical FFM summary of personality description. By contrast, RST is arguably the personality theory applied within the context of work (Furnham & Jackson, 2008) that has the most empirical support: in neuroscience especially, it is certainly the best articulated in terms of brain-behavioral systems. RST is built upon three postulates: (a) differences in specific brain structures underpin individual differences in sensitivity to perceived gain and loss; (b) these valuations lead to stimuli serving as attractors and repulsors; and (c) depending on the relationship between attractors/repulsors (i.e., strength and conflict potential), there is activation of three neuropsychological systems of approach, avoidance, and conflict resolution. Although debate continues around details of the theory, the broad dimensions of approach and avoidance are widely acknowledged as fundamentals in human behavior (Elliot, 1999).

Therefore, any viable account of workplace motivation needs to consider five processes: Two input systems for the valuation of stimuli/events (gain and loss) which define them as attractors/repulsors, and three output systems that regulate behavior (approach, avoidance, and conflict). Formally, "motivation" is the outcome of gain/loss valuation which, then, activates specific effector output systems: "Drive" is the net product of the interplay of these motivational forces – if this statement is true, then we should be able to understand the underlying psychological dynamics of "drive" by understanding each of these systems and how they function together.

Reinforcement Sensitivity Theory (RST): Systems

Stimuli, events, and the like, only exert motivation pulls and pushes once their significance has been evaluated – a statement seemingly of innocent content until we see the theoretical importance of it. Elsewhere, Corr and McNaughton (2012) have developed this theory to show how this is a precondition to understanding how neuropsychological output systems are activated. Observation of stimuli that act as attractors or repulsors bring three output systems into play: *Behavioral Approach System* (BAS), *Behavioral Inhibition System* (BIS), and *Freeze-Fight-Flight System* (FFFS) (Gray & McNaughton, 2000).

The *attractor* BAS responds to stimuli evaluated as rewarding (gain, including stimuli that signal the *relief* of non-punishment), and it initiates and controls all reward-seeking behavior. As such, the BAS is associated with anticipatory pleasure and hopeful anticipation. At dysfunctional levels, BAS-related traits (e.g., sensation seeking) map onto addictive behaviors (e.g., pathological gambling) and various varieties of high-risk and impulsive behavior. At normal levels of operation, this system reflects what we colloquially term "motivation" or "drive." In contrast, the *repulsor* FFFS responds to stimuli evaluated as punishing (loss; including stimuli that signal the *frustration* of non-reward); it is associated with distress, fear, and avoidance, and with a general moving away from approaching stimuli of all kinds. As we shall see, these two systems work together to produce *net* drive and level and quality of performance. In addition, to performance, these personality factors also relate to work-related health (van der Linden, Taris, Beckers, & Kindt, 2007), which we should expect also to impact upon performance.

When stimuli are evaluated exclusively as either an attractor/rewarding or as repulsor/punishing, then the BAS and FFFS, respectively, take charge of the behavioral machinery (and influence separate, but related, affective, and cognitive processes). However, in many situations, especially in the workplace, both the BAS and FFFS may be simultaneously activated and, in this situation, control of behavior will reflect the *subtraction* of one motivational impulse from the other – this produces *net* drive. However, in situations where no single behavioral output is sufficient to deal with the evaluation of perceived attractor/reward and repulsor/punishment – that is, where there is a *goal conflict* – then a third system is invoked, namely the BIS. Although the BIS can be activated by the presence of incompatible behaviors of similar strength (e.g., approach and active avoidance in the classic Miller approach-avoidance conflict situation), more generally the BIS is sensitive to conflict between *goals*, which can be abstract and not overtly behavior based.

Consequently, the task of the BIS is to detect and resolve goal conflicts. In doing this, it inhibits any pre-potent approach and avoidance behavior that the BAS or FFFS was about to carry out, but it allows them to continue with *cautious* behavior (involving risk-assessment) where the avoidance tendency is somewhat less than the approach tendency (Gray & McNaughton, 2000). BIS operation heightens risk-assessment, recruiting other processes that are experienced as rumination and worry. During this time, the FFFS activates, increasing negative affect and the negative valuation of conflicting stimuli, resulting in perceiving the world to be a more dangerous and threatening place.

The BIS activates a number of psychological processes of relevance to the workplace: Risk-assessment, checks for sources of threat, and inhibition of ongoing behavior. In normal operation, this is an adaptive process of caution, weighing up all the possibilities (Perkins & Corr, 2006). However in hyper-BIS individuals, its activation leads to a marked decrement in ongoing work performance, consisting of doubt, indecision, worry, and engagement of time-wasting "displacement activities" (e.g., gossip, or too-frequent checking of emails; or seeking reassurance and support from social media). These processes may be expected to exert extensive effects on the efficiency of workplace behavior but may also lead to the avoidance (e.g., by procrastination) of unpleasant tasks. Nonetheless, the processing of goal conflict by the BIS, although experienced as negative, can lead to adaptive solutions to existing "problems," especially in cognitively demanding tasks (Perkins & Corr, 2014) and, possibly even, creative ones where mulling over solutions is required (Perkins, Arnone, Smallwood, & Mobbs, 2015).

In summary, there are, at least, two "avoidance" systems, one for simple active avoidance/escape (FFFS), and one for goal conflict (passive avoidance; BIS). FFFS and BIS often interact with the reward (BAS) system. These interactions can be subtractive (e.g., FFFS-BAS) or inhibitory (e.g., BIS-BAS), but may even be additive (e.g., FFFS-related flight to a place of safety would also entail the BAS in a unified action; see Boureau & Dayan, 2011), especially in their generation of arousal.

INTEGRATING RST WITH EMPLOYEE PERFORMANCE

Given the above analysis, a person's dispositional level of general workplace drive is a key characteristic that differentiates outstanding performers from under-performing ones, particularly in roles where a focus on results makes a substantial difference to organizational success, such as professional and senior management positions (however, to varying degrees, these arguments apply to all levels of employment).

Early evidence of the value of drive in managerial roles was provided by Kaplan (1991), who conducted a rigorous six-year qualitative study of 42 senior executives from Fortune 500 companies. Using "biographical action research," Kaplan conducted intensive interviews with participants and their peers, superiors, subordinates, friends, and family, to develop a grounded theory of executive performance. Kaplan identified a common trait that characterized top-performing executives, a factor termed "expansive character," which reflected a "deep unifying structure that encompasses the individual's nature", reflecting their "crowning purpose in life" (p. 50). This trait is defined as "considerable drive to achieve and advance that manifests itself in extreme persistence, energy, confidence and resourcefulness" (p. 58). Kaplan also suggests that expansive individuals are concerned with gaining mastery over the environment and having excessive ambition for accomplishment; and Kaplan goes on to suggest that "expansiveness" is a theory of motivation, arguing that it is overwhelmingly related to high productivity and performance.

A central aspect of Kaplan's arguments is the focus on drive and energy, so it is surprising that the drive-linked traits identified in RST, and related research, have been rarely examined with respect to leadership research. However, there is considerable leadership research examining related traits, as summarized by Hoffman, Woehr, Maldagen-Youngjohn, and Lyons (2011). In their meta-analysis, they found that one of the traits Kaplan identified, energy, was one of the strongest predictors of leader effectiveness ($r = .29$). As a trait, energy has logical links with BAS. On the other hand, self-monitoring is a trait that exemplifies the behavioral control associated with BIS, and is also one of the strongest predictors of leader effectiveness ($r = .19$). So, although there is little direct evidence, there are strong hints that RST traits will be linked with leadership.

Aspects of Drive

In studies of leadership, drive is described in several different ways. One is as a need for power or social ascendancy (Bentz, 1985; Kaplan, 1991; Kotter, 1982), another is as achievement orientation (Bray, Campbell, & Grant, 1974; Kaplan, 1991; Kotter, 1982; Lombardo, Ruderman, & McCauley, 1988), and yet another way is as energy, effort, and activity levels (Hogan, Raskin, & Fazzini, 1990; Kirkpatrick & Locke, 1991; Locke, 1997). All of these approaches have in common that drive is about seeking the rewards of life – although the precise form that these rewards take differ between individuals.

In consideration of these ideas, RST suggests that a given level of drive may be motivated by different processes in different people. For example, in one person, the positive outcomes of high BAS sensitivity may be moderated by a strong FFFS (subtracting effect) or BIS (inhibiting effect). In a different person, a similarly low level of drive may be motivated by a lack of BAS drive, irrespective of the FFFS and BIS. In these various cases, different forms of initiatives would be needed to motivate performance because, although the level of manifest drive may be the same, their causal roots will be quite different (in the former case, the reduction of fear/anxiety, while in the latter case, more salient and stronger rewarding stimuli). The different combinations, and corresponding personality types, of FFFS, BAS, and BIS, are shown in Table 1 (and discussed further below). This is one of the major strengths of applying a theoretically based neuroscience model of motivation and personality within organizational psychology: It allows much more nuanced predictions about appropriate responses to individual performance issues than can be obtained by merely "reading off" summary descriptions obtained from models such as the FFM.

BAS AND WORKPLACE BEHAVIOR

Deeper consideration provides an important example of the value of RST for analyzing workplace phenomena. A high level of drive and exploration

Table 1. Personality Types Derived from Combinations of BAS, FFFS, and BIS Factors in the Workplace.

BAS−			
FFFS−		FFFS+	
BIS−	BIS+	BIS−	BIS+
Low drive for reward; low punishment sensitivity; low goal conflict detection (low anxiety). Weakly driven to achieve results, without fear of failure, and with a lack of awareness for *how* the results are achieved.	Low drive for reward; low punishment sensitivity; high goal conflict detection (high anxiety). Weakly driven to achieve results, without fear of failure but with an adequate awareness for *how* the results are achieved.	Low drive for reward; high punishment sensitivity; low goal conflict detection (low anxiety). Weakly driven to achieve results but with a strong fear of failure and a lack of awareness for *how* the results are achieved.	Low drive for reward; high punishment sensitivity; high goal conflict detection (high anxiety). Weakly driven to achieve results, but a strong fear of failure, but with an adequate awareness for *how* the results are achieved.
"Apathetic"	*"Indecisive"*	*"Avoidant"*	*"Cautious"*
BAS+			
FFFS−		FFFS+	
BIS−	BIS+	BIS−	BIS+
High drive for reward; low punishment sensitivity; low goal conflict detection (low anxiety). Strongly driven to achieve results without fear of failure, but has a lack of awareness for *how* the results are achieved.	High drive for reward; low punishment sensitivity; high goal conflict detection (high anxiety). Strongly driven to achieve results without fear of failure, but with an adequate awareness for *how* the results are achieved.	High drive for reward; high punishment sensitivity; low goal conflict detection (low anxiety). Strongly driven to achieve results but with a strong fear of failure and lack of awareness for *how* the results are achieved	High drive for reward; high punishment sensitivity; high goal conflict detection (high anxiety). Strongly driven to achieve results with a strong fear of failure but with an adequate awareness for *how* the results are achieved
"Reckless"	*"Striving"*	*"Tentative"*	*"Volatile"*

Notes: Cognitive ability should be expected to modify the effects of these motivational types. For example, low and high cognitive ability should have different performance outcomes for the "striving" type. However, for other types (e.g., "Apathetic" and "Cautious") cognitive ability would probably not mitigate the deleterious motivational effects on performance. The type of occupation is important too, as some (e.g., artistic environments) may facilitate the creative energy of the "Volatile" type, although a considerable degree of social support, of a non-confrontational type, may be needed and would, by itself, impose a cost on organizational efficiency – although a "Volatile" genius may be worth nurturing. Also, see text.

in the workplace will be heavily influenced by the BAS and for this reason it would be worthwhile delineating it in a little more detail. First, there are good reasons to think that the BAS is multidimensional in nature (Carver & White, 1994; Corr, 2015), and this might give some clues to its influence on workplace motivation and performance.

Now, the primary function of the BAS is to move the person along the temporo-spatial gradient, from a *start state* (e.g., the idea of a new project), toward the *final biological reinforcer*. For example, completion of project goals and obtaining rewarding feedback acts as a reinforcer, as experienced by sales-people at the end of successful sales presentations, which may be why BAS-linked personality is associated with greater sales performance (Barrick et al., 2001). In this context, the successful presentation is the reinforcer at this point on the temporo-spatial gradient. To move along the temporo-spatial gradient to the final biological reinforcer, some form of "sub-goal scaffolding" is needed (Corr, 2008b). This process consists of: (a) identifying the final outcome (e.g., closing the sale); (b) planning behavior (e.g., preparing sales pitch); and (c) executing the plan (i.e., performing in the sales situation). Therefore, these *approach* behaviors lead to the final desired reinforcer-outcome (e.g., getting the contract) by entailing a series of sub-processes, some of which may oppose each other. Examples of potentially conflicting sub-processes include pressuring versus listening to the customer, and enacting the planned presentation versus responding to customer reactions and questions. Managing these conflicting sub-processes requires the oversight of the BIS. We have used a sales scenario to illustrate this process, but the separate steps apply to any form of goal-directed behavior.

Studies that have examined reinforcement sensitivity in this sphere have been rare, although this state of affairs is gradually changing. Some authors have discussed the subject (Furnham & Jackson, 2008; Hutchison, Burch, & Boxall, 2008; Jackson, 1999, 2001; Johnson, Change, Meyer, Lanaj, & Way, 2013; van der Linden et al., 2007), and Burch and Anderson (2008a, 2008b) have included Gray's FFFS, BIS, and BAS in a causal model of work-related behavior and performance. However, for the most part, these research efforts have only tackled parts of the overall picture and all have used the original two-factor model of RST (BIS/BAS; Gray, 1982), which has long been superseded by the more sophisticated theoretical account that delineates more fully the FFFS, BIS, and BAS (Corr & Cooper, 2016; Corr & McNaughton, 2012; Gray & McNaughton, 2000; for a summary, see Corr, 2015).

Especially encouraging of the utility of RST, and the need to consider some degree of complexity (e.g., the interplay of attractor and repulsor systems), is Hutchison, Burch, and Boxall (2013) who reported that, in terms of senior executive performance, the optimal personality is a combination of high BAS *and* low BIS. This finding makes considerable sense in terms of the theoretical expectation of RST processes in the workplace. However, in this context, it needs to be noted that too low a level of the BIS should be expected to be deleterious because the individual would not be sensitive to goal conflict, which is often the necessary first step to resolving problems.

Goal Setting and Social-Cognitive Aspects of Motivation

In the IO literature, there has been considerable research analyzing the motivational factors and their impact upon performance, most notably goal-setting theory (Locke & Latham, 1990, 2002, 2004) and the social-cognitive theory of self-regulation (Bandura, 1991). It is not surprising, therefore, that existing attempts to look at workplace motivation from a dispositional perspective usually focus on one or the other of these main theories. Important examples are Dweck and colleagues' considerable work on goals and especially "goal-orientation" (Dweck & Elliott, 1983), and Judge and colleagues' work on the trait of "core self-evaluation" (Erez & Judge, 2001; Judge & Bono, 2001).

Goal-setting theory is one of the most powerful explanations of worker performance (Locke & Latham, 2002) and is based on the idea that goals guide behavior (performance) by directing attention. Core self-evaluation (CSE) is a personality cluster made up of locus of control, emotional stability, self-esteem, and generalized self-efficacy. Whereas goals guide worker efforts toward success, CSE plays a similar role to *expectancy* of success in integrated theories of motivation, such as that proposed by Steel and König (2006). Consistent with this approach, CSE has shown moderate power to predict job performance (Erez & Judge, 2001).

Despite the obvious parallels between goal-setting/CSE and RST, there have to date been only a few studies that have explored the link between these motivational constructs and personality factors. For example, both avoidance motivation and CSE are related to trait neuroticism, the broad personality dimension that reflects the degree to which a person experiences their environment as threatening and outside of their control (Hogan, Hogan, & Warrenfeltz, 2007). However, trait neuroticism also reflects both the FFFS and BIS of RST (it is a derivative factor of the dimension of punishment sensitivity; McNaughton & Corr, 2004). Neuroticism has been found to be significantly related to "avoidance motivation" (Smits & Boeck, 2006), although as we have seen above in the context of RST, this is an ambiguous concept and entails the actions of both the FFFS and BIS. Similarly, neuroticism is a facet of the trait core self-evaluation, so there does appear to be a common linkage.

RST and Goal-Orientation

Although much of the work exploring goal-setting within organizations has focused upon the process by which goals have been communicated and adopted (Locke & Latham, 2002), goals have also been examined from an individual differences perspective. Specifically people vary with respect to the types of goals they tend to focus upon, which is typically referred to as their goal-orientation (Dweck & Elliott, 1983). Elliot and Thrash (2002) showed that performance goals can be divided into two categories: performance-approach goals, which focus on attaining competence; and performance avoidance goals, which focus on avoiding incompetence. As predicted by RST, they found that the BAS dimension is related to a tendency to set performance-approach goals, while the BIS dimension is related to a tendency to set performance (approach and avoidance) goals. In two cross-sectional studies, Poortvliet, Anseel, and Theuwis (2015) found that employees' work-related mastery-approach goals (i.e., the striving to improve one's performance at work) are positively related to work engagement; whereas, employees' work-related mastery-avoidance goals (i.e., the striving to avoid performing worse than one aspires to) were related to job detachment and fatigue. All of this suggests that there are links between the approach/avoidance dimensions, core self-evaluations and goal-orientation. (It should be noted that in these studies the "BIS" has not been differentiated into FFFS and BIS components proper, so "BIS" here must be interpreted as general punishment sensitivity; for a discussion of this matter, see Corr, 2015.)

Once the BAS has influenced a person's decision that they are capable of attaining a particular reward, it then facilitates, by recruiting necessary processes, the achievement of that reward. This process involves organizing cognitive resources, planning and initiating behavioral sequences that will enable the person to reach their goals, the "sub-goal scaffolding" discussed previously (Corr, 2008b). The continual, emotionally driven focus on rewards causes a person to set particularly difficult goals and persist in achieving them. Long-term views may be taken due to the drive to achieve, hence the predisposition for a long-term learning goal-orientation as well as a shorter term performance-approach orientation (Elliot & Thrash, 2002).

In terms of Elliott and Thrash's (2002) findings that avoidance motivation is related to performance goal-orientation, it makes sense that punishment sensitivity would influence such a preference because of the potential for negative feedback if these goals are not achieved. Because of the focus on punishment, a person with strong FFFS sensitivity would be likely to set easier goals to avoid failure, which would in turn lead to lower performance. In particular, punishment-sensitive people may be susceptible to negative emotions in response to memories of previous failures and threats of future failures, potentially making them feel vulnerable, which would affect their feelings of control over the situation. However, a strong BIS may enable punishment-sensitive individuals to refocus by employing their self-regulatory skills leading to enhanced performance (cf. Kurzban, 2016).

There has been a recent surge of interest in the mediating processes between disposition and workplace performance. Much of this research has been conducted using personality traits as predictors, testing motivational mediators, such as self-efficacy, attributional style, or goal setting. The findings suggest that personality traits are, indeed, mediated by these sorts of constructs (Chen, Gully, Whiteman, & Kilcullen, 2000; Jackson, 2001; Locke & Latham, 2002). While some personality traits – mainly conscientiousness and neuroticism – have been shown to be related to work performance (Barrick & Mount, 1991; Hogan & Holland, 2003), the trait theories used in such research provide no explanation as to why. In addition, predictive validities are moderate, so there is plenty of scope for reinforcement sensitivity theory to improve on the validity provided by personality, and to provide a fuller explanation of the dispositional side to motivation.

Finally, RST can be used to explain the findings that disposition is related to job attitudes (Newton & Keenan, 1991) and to job satisfaction (Furnham, Petrides, Jackson, & Cotter, 2002), which in turn are related to performance (Judge, Thoresen, Bono, & Patton, 2001). RST helps to explain how it is that some people are naturally more satisfied than others in the job, due to predisposition to positive emotional reactions, and will therefore naturally have positive attitudes, and demonstrate resulting outcomes such as organizational citizenship behavior and organizational commitment. Once again, this all stems back to perception and the encoding of environmental stimuli in positive or negative ways. Consequently, RST provides an individual differences foundation for a range of diverse motivation-related theories, where these are treated as facets or contributing subfactors.

PUTTING RST TO WORK

Individuals with a strong BAS possess a heightened approach drive (all else being equal) but this motivational propensity should be expected to be modulated by the activity of the FFFS and BIS. These interactions between the various components of RST, along with the personal specificity of what counts as an attractor or repulsor, mean that links between RST traits and organizationally relevant outcomes will be complex. With these caveats in mind, it should still be expected that the BAS will have an important main effect on workplace performance, with high BAS predicting high productivity and low BAS predicting low productivity: Without a reasonably strong BAS there would be no "will do" or impetus for action. Consistent with this, the aspect of the FFM that is most closely associated with BAS, namely extraversion, is reliably (if modestly) associated with work performance, especially in occupations in which performance reflects an individual's willingness to persist in the face of social resistance, such as that experienced by sales-people and managers (Barrick et al., 2001). We suggest that a person's general level of FFFS/repulsor motivation moderates the effects of BAS, sometimes in decisive ways (some positive, some negative). A healthy level of FFFS sensitivity should, indeed, temper high BAS, allowing more effective decision-making by highlighting the aversive outcomes of making a wrong decision. Here, it is interesting to note that Perkins and Corr (2006) found that, in a group of military personnel and business managers, neuroticism-related worry enhanced performance in the more cognitively able, arguably because they directed their risk-assessment toward job-related factors rather than self-focused worry. An excessively strong FFFS, in contrast, would increase simple avoidance motivation and escape from potential loss – a loss aversive disposition – or a defensive panicky type of action in other situations (where immediate decisions are needed). Indeed, excessive punishment (FFFS/BIS) sensitivity would paralyze a person's drive for results. Conversely, if punishment sensitivity is too low it could lead to a person's drive becoming uncontrolled and disinhibited: Yet another route to BAS-redirected reckless and capricious behavior.

Activation of the FFFS will generally subtract from BAS effects; if sufficiently intense, this will lead to a conflict activating the BIS resulting in cautious and indecisive action. Although in some organizational contexts this may well be adaptive behavior, its long-term activation should be expected to impair performance. Specifically, goal conflict in BIS theory includes conflict between two equally balanced, but incompatible, goals and intriguingly, these goals can both be attractors (e.g., business strategies) which we should expect to impair performance, especially if the negative consequences of making the wrong decision is evaluated as a form of, saliently aversive, loss. Added to this intensity of these effects is the appraisal of these outcomes for employee's own status and standing in the organization. Consistent with this, individuals who are high on the BIS-related FFM dimension of neuroticism (the opposite end of which is commonly labeled as emotional stability), tend to have lower performance in all occupations (Barrick et al., 2001).

It is possible that if a person has extremely low BAS, their levels of FFFS and BIS make little difference, as they would have low drive in the first place and little biological capability to activate behavior. Even with a healthy FFFS/BIS, it is questionable whether the risk of disciplinary action (e.g., punishment) in the workplace could actually jolt a person into action if the BAS were underactive. Such action would serve only to inhibit behavior further, and perhaps lead to counter-productive behavior of an opposition and defiant kind.

This brief analysis can do little more than to illustrate the potential complexity of the relationships yet, as we have shown in Table 1 it is possible to tabulate the outcomes of low and high mixtures of the FFFS, BIS, and BAS. With these initial propositions in mind, we now turn to the available research for more concrete suggestions of how RST might provide a dispositional framework for workplace motivation.

When thinking about personality and motivational types in terms of combinations of the FFFS, BIS, and BAS, several factors spring to mind. The first is the nature of the environment. For example, in a highly supervised environment where close monitoring is possible, then even a low BAS level can be encouraged to work to a satisfactory standard – being "apathetic" and "indecisive" are characteristic ways of behaving (and feeling and thinking) when these types are left to their own devices – but they most certainly would not be self-starters and resourceful. However, in loosely constrained environments where there is a wide latitude of choice, then high (but not too high) BAS along with a non-crippling forms of FFFS and BIS activity are needed.

As mentioned elsewhere, cognitive ability is likely to be important, especially in non-manual professions, but even in such low skill occupations it is not unimportant. For example, the "striving" type may or may not achieve anything of substance if they their motivational "will do" is not coupled to a cognitive "can do." And much the same goes for the other personality/motivational types.

Therefore, when thinking about the quantity and quality of performance, knowing someone's personality/motivational type is not *sufficient*, but as we have argued throughout this chapter, it is *necessary*. In a reworking of Blumberg and Pringle's (1982) famous equation, it is possible to identify the role of the likely individual differences factors in more formal terms, as follows:

$$P = \text{MT} \times \text{cognitive ability} \times \text{environment} + e$$

where P is performance (quantity × quality), MT – motivation type, *Cognitive ability* is general intelligence and any specific forms of ability required of by the job, *Environment* is the situational factors that impact upon the employee (e.g., degree of supervision, but also incorporating Blumberg and Pringle's *opportunity*), e is the statistical error.

As the relationships between MT, cognitive ability, and environment are multiplicative functions, a low value of one of these components would significantly reduce P, irrespective of the value of the other components.

CODA: THE DARK SIDE OF WORKPLACE MOTIVATION

But all is not rosy in the organizational garden. Counter-productive, immoral/criminal, and seemingly paradoxical, workplace behaviors have attracted much less attention than their ubiquity and importance deserves. In wider psychology, there has been a resurgence of interest in the "dark side" of personality, often couched in terms of the triad of psychopathy, narcissism, and Machiavellianism (O'Boyle Jr, Forsyth, Banks, & McDaniel, 2012). These dark characters can be found strolling workplace corridors, irrespective of the quality of management – the psychopathic type, perhaps the most common of the dark personalities, has been referred to as "snakes in suits" (Babiak & Hare, 2007). Here though, we are concerned with more mundane forms of dark behavior that thrive in poorly managed environments. We argue that perplexing behaviors – by which is usually meant, behaviors that do not conform to normal theoretical understanding – are, in fact, just as explicable as more straight-forward productive behaviors of the type the yields to analysis along RST lines.

In particular, we contend that ineptly or neglectfully managed work environments that do not encourage positive motivation, and do not entail appropriate sanctions designed to align worker behavior with organizational aims, will foster such dark behavior. In effect, a psychological vacuum is created that is filled with counter-productive behaviors that make people very busy, often destructively so, but achieving very little of any good (a human form of displacement activity, seen in other animals during times of stress). Such dark personality types will engage in personally BAS-satisfying, but organizationally speaking, counter-productive behaviors (e.g., establishing their own modes of work behaviors, placing obstacles in the way of others, gaining control over and manipulating them, as well as systems such as financial procedures and channels of communication and influence). However, these facilitative structures and cultures do not affect the amount of positive performance displayed by "dark" personalities (O'Boyle et al., 2012), which is consistent with the foregoing analysis in that such personalities are likely to relatively self-motivated, with high BAS in the first place.

The point we wish to emphasize with regard to "dark motivation" is that high drive can be negatively as well as positively directed. Some people, especially those equipped with tough-mindedness, devious, Machiavellian, and an entitled, ways of thinking and feeling will engage in behaviors aimed at gaining, maintaining, or retaining their sense of perceived control: These motivated behaviors meet their own goals, and in this sense are purposively, BAS-mediated, directed. Seen in this theoretical light, such individuals are little different to other personality types in their need to achieve their BAS goals. They are, however, very different in terms of their route to achieving such reward. In terms of behavior modification though, aligning BAS-related behaviors with organizational aims – a worthy but often difficult trick to pull off – or by removing such people from positions of influence, are the two main ways to reduce their negative impact upon the organization and other employees.

CONCLUSIONS

Our discussion has highlighted a number of propositions, based on a fundamental neuroscientific theory of motivation and personality that have a direct and influential bearing on a person's innate level of drive and workplace performance. Specifically, we contend that the roles of the BIS, FFFS, and BAS are useful in understanding work motivation, providing novel insights that are unobtainable from more descriptive personality models. Further, our analysis shows that a basic neuroscience of motivation can be extended to the work environment to provide a general framework of employee motivation, something that has been lacking in the industrial and organizational literature.

Specifically, we contend that, as main effects, the BAS predicts high performance and the FFFS low performance; however, we have seen that it is the *interplay* of these two processes, along the BIS, that determines actual (net) performance. We have also mentioned, but not elaborated upon, the modifying role of cognitive ability, higher levels of which have been shown to enhance the performance of more anxious (i.e., BIS-active) employees (e.g., Perkins & Corr, 2006 – for a discussion of the positive side of negative emotions, see Perkins & Corr, 2014). As presented in Table 1, specific combination of the FFFS, BAS, and BIS yield the personality-based motivational "types" found in the workplace. Here, it is important to note that unrestrained BAS is maladaptive (the "reckless" type in Table 1), especially in producing toxic, destructive leadership behaviors (Kaplan, 1991).

Table 1 shows type combinations based on relatively low and high trait values, but most people lie between these extremes so, in practice, the work-related motivation-performance picture will be less clearly crystallized than suggested here; however, the same psychological dynamics should be expected to apply. It may be speculated that it is at these average motivation values than typical workplace initiatives work best – those at the extreme ends of these distribution are, motivationally speaking, more set in their ways.

We acknowledge that, at this stage, our propositions are theoretically based and not a little speculative. However, the basic constructs we employ are widely accepted in psychology, especially the neuroscience of motivation and personality. We believe they open up a completely new side to motivational theory that calls for future testing. If our propositions were shown to be correct, psychometric tests of reward/gain and punishment/loss sensitivity could provide organizations with a good indication of which employees are most likely to demonstrate outstanding performance and also which employees could be the most driven to attain and succeed in key positions. However, as we also highlight, motivation disposition will interact with situational factors to determine behavior. Our ideas also call attention to the need to build work environments were high levels of motivation are directed to organizational objectives, and not to counterproductive behaviors.

If nothing else, the theoretical framework we have proposed provides a way of thinking about workplace behaviors and their bases in the neuroscience of motivation, and a set of testable predictions that go far beyond the merely descriptive, correlational studies that currently dominate personality research within organizational settings.

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“YOUR CHOICE” MOTIVATES YOU IN THE BRAIN: THE EMERGENCE OF AUTONOMY NEUROSCIENCE

Kou Murayama, Keise Izuma, Ryuta Aoki and Kenji Matsumoto

ABSTRACT

Studies in psychology have long revealed that making personal choice involves multiple motivational consequences. It has only been recent, however, that the literature on neuroscience started to examine the neural underpinnings of personal choice and motivation. This chapter reviews this sparse, but emergent, body of neuroscientific literature to address possible neural correlates underlying personal choice. By conducting the review, we encourage future systematic research programs that address this topic under the new realm of “autonomy neuroscience.” The chapter especially focused on the following motivational aspects: (i) personal choice is rewarding, (ii) personal choice shapes preference, (iii) personal choice changes the perception of outcomes, and (iv) personal choice facilitates motivation and performance. The reviewed work highlighted different aspects of personal choice, but indicated some overlapping brain areas – the striatum and the ventromedial prefrontal

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cortex (vmPFC) – which may play a critical role in motivational processes elicited by personal choice.

Keywords: Self-determination; reward network; social neuroscience; intrinsic motivation

In our daily life, we make numerous personal choices. These include choices between specific behaviors (e.g., "Should I fight or run away?") as well as choices between higher level goals (e.g., "Should I go to a graduate school or get a job at a company?"). We also encounter various situations where we are not allowed to make a personal choice and are forced to engage in a specific option for various reasons (e.g., "I have to work for the development of this software, because this is the current priority of our company"). Do you think you would have different reactions when you can make your own choice as opposed to when you are forced to take a specific option? The answer is likely to be yes (we believe). In fact, as reviewed later, there have been numerous empirical studies supporting the idea that personal choice and forced-choice would have different impacts on motivation and performance (for a review, see Patall, 2012).

Importantly, despite the voluminous research on choice and motivation in the literature of psychology, the role of personal choice in motivation has attracted much less attention in neuroscience (Leotti, Iyengar, & Ochsner, 2010). This is partly due to the fact that neuroscientific theories of motivation often base their models on the standard reinforcement learning model (Sutton & Barto, 1998), which is an extended version of the traditional models of behaviorism. According to the standard view of behaviorism, people's motivated behavior is solely determined by the contingency between the action they take and the delivery/absence of rewards. That is, this traditional view is basically indifferent to whether the choice of action was made out of one's own will (i.e., personal choice) or determined by others (i.e., forced-choice). Therefore, from a perspective of behaviorism and reinforcement learning model, it is not as obvious as we suppose that personal choice and forced-choice would elicit different psychological process in human behavior. Indeed, it has only been recently that researchers proposed a reinforcement learning model that formally incorporated how personal choice (as opposed to forced-choice) can bias the decision-making process (Cockburn, Collins, & Frank, 2014). To be clear, there is a vast amount of neuroscientific research that has addressed the factors that guide people's choice or decision making. Also, reinforcement learning models are often considered as autonomous models, in that the model formulates how agents can learn optimal decision making in dynamic environments with trial and errors, without assuming any a priori knowledge. Some forms of reinforcement learning are indeed remarkably powerful to actively learn optimal choices in very complicated environments (especially, the so-called model-based learning; Daw, Gershman, Seymour, Dayan, & Dolan, 2011; O'Doherty, 2012; Sutton & Barto, 1998; see also Tolman, 1948). Nevertheless, these models do not consider that agents have the natural inclination to give special privileges and preferences to personal choice over forced-choice. Thus, in neuroscience, the idea that "your choice" would make a difference is still a new topic which has much room for future research.

The purpose of this chapter is to provide an overview of the sparse, but emergent neuroscientific literature on the neural correlates underlying the psychological effects of personal choice. The research we will cover has been studied rather independently, and these studies have rarely been brought together under the topic of personal choice and motivation (for an exception, see Leotti, Cho, & Delgado, 2015). Given the limited number of the relevant research, we do not provide an integrative view about the neural mechanisms underlying personal choice – time is not ripe yet. By putting together different lines of neuroscientific research related to personal choice, however, we are hoping to highlight the coherence and the importance of the topic in a broader sense, calling for future systematic research programs on this topic.

PERSONAL CHOICE IS REWARDING

Making a personal choice involves cognitive effort. To decide between options, people have to carefully consider both the positive and negative potential consequences of the options and determine how to weigh these qualitatively different aspects. This is a demanding task. In fact, Vohs et al. (2008) showed that making a series of choices between consumer products or university courses produces the depletion of self-regulatory resources, impairing the performance of the subsequent self-regulation behavior (e.g., drinking a bad-tasting drink). Also, generally speaking, people do not like demanding tasks or exerting mental effort, and people do indeed avoid or devalue effortful tasks (Botvinick, Huffstetler, & Mcguire, 2009; Kool, Mcguire, Rosen, & Botvinick, 2010). Choice is demanding and people do not like demanding tasks. A logical consequence of these two propositions is, of course, that people should hate making personal choices. However, the reality is opposite – people *love* personal choices. People seek opportunities to decide on their own will, and people would become much happier if they had an opportunity to make their own mind. We are natural-born choice seekers.

Some may argue that people like choices because the freedom to choose can potentially increase the likelihood to obtain better outcomes. This can explain part of the reason why people like personal choice. But the literature in psychology has found that people prefer, or value, the freedom to choose even if the choice outcome is irrelevant with their choices or if choice outcomes are inconsequential (see also Bartling, Fehr, & Herz, 2014 on this topic in the literature of economics). For example, in Suzuki's (2000) study, participants were asked to select a two-choice task or single response task. In the two-choice task, participants can select one of the two cards, whereas in the single response task, participants have to select the card presented on the screen. Participants can receive points based on what they found on the card they eventually selected. They found that participants preferred to select the two-choice task even if they knew their expected amount of points had nothing to do with their choice (see also Suzuki, 1997). Bown, Read, and Summers (2003), in their paper titled "*the lure of choice*," showed that participants are more likely to select an item when the item was initially part of a choice than when it was presented on its own. Perdue, Evans, Washburn, Rumbaugh, and Beran (2014) revealed that even capuchin monkeys prefer the option that allows them to select the order of task completion in comparison to the option that provides a pre-determined task order.

Given these findings, it is straightforward to hypothesize that choice has some inherent rewarding value. Previous neuroimaging studies revealed the brain network that supports people's preference, or value (Kable & Glimcher, 2009; Knutson & Cooper, 2005; for a meta-analysis, see Bartra, McGuire, & Kable, 2013). These brain areas are typically called the "reward network," and are deemed to play a pivotal role in representing and updating various types of subjective valuation. The reward network includes the ventral tegmental area (VTA), the striatum (e.g., nucleus accumbens, caudate), and the ventromedial prefrontal cortex (vmPFC).

The hypothesis that choice entails reward value can be directly tested by using neuroimaging. In the experiment conducted by Leotti and Delgado (2011), participants were presented with a symbolic cue that informs whether they can make a choice or not in the upcoming trial. In the choice trials, participants could freely choose one of the keys. In the no-choice trial, participants were forced to accept a computer-selected key. When participants pressed a key, they received feedback regarding the amount of monetary reward they obtained. Critically, all the keys had the same expected reward value – therefore, the choice was actually irrelevant to the actual consequences, and in fact all participants earned approximately the same amount of monetary rewards. Nevertheless, like the previous behavioral studies (e.g., Suzuki, 2000), participants indicated preference for the cue that predicts choice trials. More importantly, their analysis using functional magnetic resonance imaging (fMRI) showed the increased activations of the bilateral ventral striatum and the midbrain in response to choice cues (as compared to forced-choice cues), indicating that the cue signaling upcoming choice had rewarding characteristics. This finding was replicated by other fMRI studies (Leotti & Delgado, 2014; Murayama et al., 2015).

Fujiwara et al. (2013) examined the rewarding nature of choice from a different angle. They put participants in a situation where participants have to select between (1) an option that would give participants a specific amount of money (e.g., 30 Japanese Yen) and (2) an option that would give participants a certain number of choice options out of which they could pick up one, everyday consumer product. This experimental paradigm allowed the researcher to gauge the value of choice as a function of the number of choice alternatives. The results showed that participants value having more choice alternatives (interestingly, some participants also exhibited preference for choice from a larger number of low-value items than a forced-choice of single high-value item), and the number of choice alternatives is positively related to the striatal activation in the brain, indicating that the rewarding property of choice increases as the number of choice alternative increases. These results suggest that people value not only the choice itself, but also the number of potential choice options.

Further elaborating the effects of the number of choice options on the activation of the reward network in the brain, recent fMRI work by Aoki et al. (2014) showed that the effects of the number of choice alternatives is also influenced by social context. In this study, participants performed a two-person choice task in which the number of choices (one, two, or four) available to a participant and a confederate was individually manipulated for each trial. Participants could earn monetary rewards by choosing a correct option, which was revealed after the choice of the participants. Importantly, they were explicitly told that the number of their available options was nothing to do with the probability of winning the outcome, and that the win or loss of the other player (i.e., confederate) was independently determined. That is, the other player's outcomes, under no circumstances, could influence the participants' probability of winning. Despite the fact that the number of choice options was irrelevant to the probability of winning, they observed an increased activation in the ventral striatum as the number of choice options available to participants increased. In addition, they also found that the equality of choice options between the participant and the other player (i.e., social equality in choice opportunity) activated another critical area of the reward network – the vmPFC (Fig. 1). These results demonstrated that choice

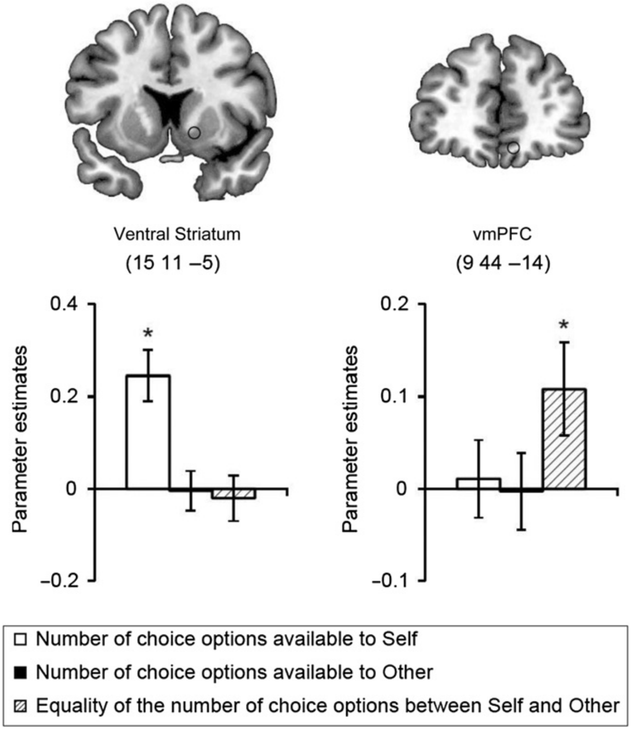

Fig. 1. Differential Effects of the Number of Choice Options Available to Participants and the Equality of Choice Options on the Ventral Striatum and the vmPFC as Reported by Aoki et al. (2014). *Notes*: The ventral striatum was significantly activated by the number of choice options available to participants, whereas the equality of choice options influenced the activation in the vmPFC. The equality of choice options was defined on the basis of the difference in the number of options between self and other (i.e., smaller difference indicates greater equality).

opportunities are processed in the ventral striatum and the vmPFC in different ways – whereas the striatum represents the absolute number of choice opportunities, the vmPFC, a key brain region previously implicated in the processing of social values (e.g., Heekeren, Wartenburger, Schmidt, Schwintowski, & Villringer, 2003; for a review, see Rilling & Sanfey, 2011), represents the valuation of equality in choice opportunity between individuals.

PERSONAL CHOICE SHAPES PREFERENCE

Choice is guided by preference. You choose to order a coffee but not a tea if you have personal preference to drink coffee over tea. No one would disagree with this presumption (i.e., "I choose it because I like it"). But what is more controversial is the idea that our personal choice can also change preference (i.e., "I like it because I chose it"). That is, once you make your personal choice to drink a coffee, you may increase your preference for coffee and decrease your preference for tea. The idea of this "choice-induced preference change" was first demonstrated by Brehm (1956), and it spawned a number of follow-up research investigations (for a meta-analysis, see Kenworthy, Miller, Collins, Read, & Earleywine, 2011).

Choice-induced preference change is typically tested through the "free-choice paradigm." In this paradigm, participants are first asked to rate (or rank) several items (e.g., music albums, posters, foods, political candidates, jobs, etc.) according to their preference (first rating task). Second, they are asked to choose between two of the items that had similar preference ratings in the first rating task (choice task). Finally, they are asked to rate their preference for the same items one more time (second rating task). Studies found that after making a difficult choice between two equally preferred items, participants' preference for the chosen item increases while preference for the rejected item decreases (e.g., Gerard & White, 1983; Heine & Lehman, 1997; Steele, Spencer, & Lynch, 1993). This process of choice-induced preference change is traditionally explained by cognitive dissonance theory (Festinger, 1957). When there is an inconsistency between preference and behavior (i.e., choosing something I don't like), it causes an uncomfortable feeling called "cognitive dissonance," which in turn motivates a person to modulate their preference in order to restore the consistency.

Several neuroimaging studies have been conducted to examine the neural mechanisms underlying choice-induced preference change (Izuma et al., 2010; Jarcho, Berkman, & Lieberman, 2011; Kitayama, Chua, Tompson, & Han, 2013; Qin et al., 2011; Sharot, De Martino, & Dolan, 2009). Specifically, these studies sought to address the following two main questions. First, by examining the brain areas associated with the changed preference, researchers tested whether choices could alter the neural representation of preference, or whether choice-induced preference change is just a superficial phenomenon seen only in the self-report (e.g., demand characteristic bias). In most of the past behavioral studies, participants' preference was assessed by self-reported questions, meaning it is possible that participants actually faked their preference which in turn could mean that the observed choice-induced preference change did not reflect the change of true preference. Neuroimaging methodology has the potential to overcome this essential (but quite common) limitation of behavioral experiments in psychology, because as indicated earlier, previous studies have revealed the brain network that supports people's preference, or value (see Bartia et al., 2013), making it possible to validate the results based on self-report questions.

Sharot et al. (2009)'s study is the first that examined the neural correlates of the preference change induced by personal choice with fMRI. Using a standard free-choice paradigm, Sharot and colleagues presented participants with many different pairs of destination names for a vacation (e.g., Thailand), and asked them to choose one of the two options based on where they would rather take a vacation. Consistent with choice-induced preference change, participants' preference changed in line with their choice – in the second rating task, destinations they chose showed increased preference, whereas destinations they rejected showed decreased preference in comparison to the first rating task. Importantly, they also observed that post-choice changes in preference were correlated with the caudate nucleus activity (within the striatum), indicating that choice-induced preference can be observed even in the neural representation of preference (see also Qin et al., 2011).

Another important question that neuroimaging studies sought to address is the psychological mechanisms underlying the choice-induced preference change. Cognitive dissonance theory (Festinger, 1957) indicates the resolution of cognitive dissonance as the key psychological mechanism. Reviewing the past literature in social neuroscience, Izuma (2013) argued that the posterior medial frontal cortex (pMFC; this area consists of the dorsal anterior cingulate cortex, dACC, the dorsomedial prefrontal cortex, and the supplementary motor area; Izuma, 2013) plays a critical role in processing cognitive inconsistency (the discrepancy between one's own belief and external input; see also Harmon-Jones, 2004). In fact, Van Veen, Krug, Schooler, and Carter (2009) adapted the induced compliance paradigm (another popular paradigm to induce cognitive dissonance) to the fMRI scanner and found that the pMFC is involved in cognitive dissonance (see also Izuma & Adolphs, 2013). As such, the activation of the pMFC in the free-choice paradigm could provide some compelling evidence for the dissonance resolution as the mechanisms of choice-induced preference change. Consistent with this prediction, fMRI studies (e.g., Kitayama et al., 2013) found the involvement of several brain regions including the pMFC when participants made a difficult choice (i.e., the choice that would induce the highest cognitive dissonance). Although we need to be cautious when inferring cognitive processes that are solely based on the neuroimaging data (the issue called "reverse inference"; Poldrack, 2006), these findings suggest a critical role for cognitive dissonance reduction in choice-induced preference change.

One important reservation for the findings discussed so far is that all of these studies have used the traditional free-choice paradigm. A recent paper by Chen and Risen (2010) pointed out an important methodological problem in this traditional paradigm, arguing that all findings from the studies using the free-choice paradigm are in conclusive (for more accessible summary, see Izuma & Murayama, 2013; Risen & Chen, 2010). In short, the critical point is that, even if participants gave similar ratings to two items in the first rating task, the fact that a participant chose a particular item in the choice task indicates that the participant actually preferred that item over the other from the outset. Thus, the higher preference ratings in the second rating task do not necessarily mean that the act of making a choice changed the true preference – the higher preference ratings in the second rating task may simply reflect the pre-existing preference. Izuma and Murayama (2013) conducted a series of statistical simulations to demonstrate the validity of the argument.

This critical methodological issue was addressed by an fMRI study reported in Izuma et al. (2010). In this chapter, the authors added a control condition where participants made a choice *after* the second rating task (see also Chen & Risen, 2010). Because the second rating was made before the choice task, rating change from the first rating task to the second rating task can be solely attributed to participants' pre-existence preferences. Thus, the presence of choice-induced preference change can be tested by comparing this control condition (called "Rate-Rate-Choose" condition) with the traditional experimental condition explained earlier (called "Rate-Choose-Rate" condition). Importantly, with this new control condition, Izuma et al. still found that (1) making a choice does indeed change self-report preference as well as its neural representation (i.e., striatum activity) and (2) the pMFC tracked the degree of cognitive dissonance (Fig. 2). These results provide a nice replication of the previous findings with a rigorous methodology, confirming the critical importance of the reward network and the pMFC in choice-induced preference change.

One of the limitations of these fMRI studies is that their findings are essentially correlational (i.e., the degree of cognitive dissonance is correlated with the degree of activation in the pMFC). Therefore, these results cannot exclude the possibility that the pMFC activity merely reflects an epiphenomenon of cognitive dissonance such as passive emotional reactions to inconsistency, rather than playing an active causal role in inducing preference change to resolve inconsistency. To directly address this limitation, Izuma et al. (2015) conducted an experiment using transcranial magnetic stimulation (TMS). TMS is a tool for noninvasive stimulation of neuronal tissue in the brain, which, in combination with cognitive tasks, allows us to examine whether the stimulated brain area has causal influences on cognition or behavior. In this study, the researchers applied a 1-Hz 25-min repetitive TMS to pMFC in order to temporarily downregulate the neural activity within that area when participants performed the second rating

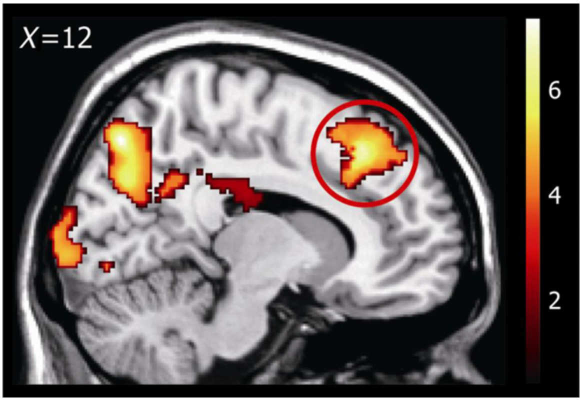

Fig. 2. An Area in the pMFC (dACC) Significantly Correlated with the Degree of Cognitive Dissonance as Reported by Izuma et al. (2010; see also Izuma et al., 2013).

task (i.e., when cognitive dissonance is produced). To address the methodological issue proffered by Chen and Risen (2010), they used a "choice-blindness" paradigm (Hall, Johansson, & Strandberg, 2012; Hall et al., 2013), which allowed the researchers to randomly assign participants' choices to preference congruent and preference incongruent conditions (i.e., they manipulated cognitive dissonance independently of the pre-existing preference). They observed choice-induced preference change in a sham stimulation condition and a control stimulation condition, but importantly, these preference changes were significantly reduced in the pMFC stimulation condition. These results indicate that the pMFC plays an active causal role in cognitive dissonance (see also Mengarelli, Spoglianti, Avenanti, & Di Pellegrino, 2015, for another TMS study on choice-induced preference change).

PERSONAL CHOICE CHANGES THE PERCEPTION OF OUTCOMES

Imagine that you achieved a project. When the project is something that you decided to work on out of your own will, you are likely to be happier than when the project was assigned by your boss. The objective value of success would not be different depending on whether you made a choice to do that or not, but the subjective value can be influenced by such a factor. This point is nicely illustrated in Cockburn et al. (2014)'s study. In this study, participants were presented with pairs of stimuli with specific expected reward values. For each trial, they selected one of the two stimuli and received or lost points. This task allows participants to learn the expected values of the stimuli over the trials. Importantly, for half of the trials (free-choice condition), participants freely selected stimuli, whereas for the other half of the trials, participants were not allowed to select a stimulus; instead, participants were forced to select a pre-determined stimulus (forced-choice condition). Unbeknownst to participants, these forced-choice trials were matched (yoked) to the trials in the free-choice condition, making it possible to directly compare the subjective value of the stimuli with and without the freedom to choose stimuli. The results showed that participants preferred the stimuli that they had freedom to choose, in comparison to the stimuli that they were forced to choose, even if these stimuli had identical rewarding history. These findings provide strong behavioral evidence that making a choice adds value to the outcome people receive.

A number of studies have demonstrated that making a personal choice changes the perception of outcomes in a variety of ways. For example, in Rose, Geers, Rasinski, and Fowler (2012), participants underwent a cold pressor task to induce pain and offered two pain-relieving treatments. Participants in the choice condition could choose one of the two treatments, whereas participants in the no-choice condition were given the treatment that the experimenter randomly determined. In fact, these two treatments were identical inert ointment mixtures and therefore choice should not have made any differences in pain perception. However, the results showed that participants in the choice condition reported significantly less pain than participants did in the no-choice condition, indicating that individuals choosing their treatment – even though it was a bogus treatment – could reduce the subjective feeling of pain compared to those who were forced to take a specific treatment (Geers & Rose, 2011; Salomons, Johnstone, Backonja, Shackman, & Davidson, 2007; see also Salomons, Nusslock, Detloff, Johnstone, & Davidson, 2014).

Although not directly testing the effect of choice, researchers also examined whether the control belief (i.e., the belief that one can control external environment) can reduce pain at the neural level. In one study (Salomons, Johnstone, Backonja, & Davidson, 2004), participants were presented with cues before painful, thermal heat. In the controllable condition, participants were instructed that they could reduce the hot stimulus to a non-painful duration by manipulating a joystick in some way, which participants needed to figure out with trial and errors. In the uncontrollable condition, participants were asked to respond as they did in the controllable condition but were instructed that their response would have no effect on the duration of the heat. Although participants were led to believe that the controllable condition could provide them with more control over the delivery of heat, participants actually received the same amount of painful thermal heat in both conditions. The fMRI results indicated that the areas of insular, secondary somatosensory, and ACC, which are commonly activated in response to peripheral nociceptive input, were also activated in response to the thermal stimulus in both conditions. Importantly, however, the activation of these areas was significantly reduced in the controllable condition than in the uncontrollable condition, suggesting that control belief can alleviate pain perception even at the neural level.

One of the most popular effects of personal choice on the subjective perception of outcome is the illusion of control. In the seminal work of Langer (1975), participants purchased a lottery ticket, and were either allowed to freely choose their ticket (choice group) or were assigned a ticket (no-choice group). The objective chances of winning were 1 in 26 in both conditions. Participants were then offered an opportunity to exchange their ticket with a new one, where the objective chances of winning would be 1 in 21. The results showed that the majority of participants in the choice group decided to keep their original lottery ticket despite that the objective chances were higher for the new ticket. These results suggest that participants overestimated the probability of winning the lottery if they had the opportunity to freely select a ticket. The act of making a personal choice favorably distorts the objective chance of success.

Research has examined how illusion of control influences the neural representation of the decision outcome. In Kool, Getz, and Botvinick (2013), participants were presented with three identical spinner dials at once, depicted as wheels of fortune. These three spinner dials represented the chance of winning. Importantly, participants were explicitly informed that the three spinners in each trial had an equal probability of a win outcome. In half of the trials, participants could choose a specific spinner (choice condition), whereas in the other half participants could indicate their preference but their preferred spinner dial was vetoed and replaced with the one that they did not choose (forced-choice condition). After the selection of a spinner, participants reported their confidence of winning using a visual analog scale. Again, participants knew that all of the spinners had an identical, objective chance of winning. However, consistent with the original illusion of control study, they found that the reported subjective probability of winning was higher in the choice condition than in the forced-choice condition. Based on these results, they hypothesized that, because participants overestimated the probability of winning in the choice condition, the choice condition would produce less "surprise" (called reward prediction error; actual reward value−expected reward value) at the positive outcome, which would manifest as the decreased activation in the ventral striatum (the brain area that represents reward prediction error; Montague & Berns, 2002). Contrary to their hypothesis, however, the choice condition and the forced-choice condition did not show differential activation in the ventral striatum, indicating that illusion of control would not influence the neural representation of reward prediction error. Instead, the choice condition showed enhanced activation in the posterior cingulate cortex, the ACC, and the middle temporal gyrus when the outcome was presented. These results indicate that the distorted probability perception due to illusion of control may be represented in a different way from reward prediction error in the brain (for a similar results, see Murayama et al., 2015; Vassena, Krebs, Silvetti, Fias, & Verguts, 2014).

PERSONAL CHOICE FACILITATES MOTIVATION AND PERFORMANCE

So far, we have discussed that personal choice would have a rewarding property, enhance the preference for the option the person chose, and bias the interpretation of the outcomes in a way that would enhance the positive feelings about the outcome. Together these findings suggest that providing a personal choice would be a good way of enhancing one's motivation and performance. In fact, there is a large body of literature in psychology showing that personal choice (as compared to forced-choice) would facilitate task motivation and performance (for a meta-analysis, see Patall, Cooper, & Robinson, 2008). The positive link between the choice and motivation is one of the central tenets of the self-determination theory (Deci & Ryan, 1985; Ryan & Deci, 2000). According to the self-determination theory, people have the basic psychological needs for autonomy and factors that satisfy the needs would enhance people's intrinsic motivation (i.e., motivation to voluntarily engage in a task for the inherent pleasure and satisfaction derived from the task itself), resulting in improved task performance and well-being. Thus, personal choice, which would provide people with the sense of autonomy and personal control, can have adaptive functioning that facilitates people's motivation and task performance.

In a classic study by Zuckerman, Porac, Lathin, and Deci (1978), university student participants were provided with puzzle pieces and asked to solve puzzles. In the choice condition, there were drawings of six configurations and they were told that they could work on three of the configurations that they chose. In the forced-choice condition, participants were provided with pre-determined drawings of three configurations (these configurations were yoked to those selected by the participants in the choice condition) and they were told to work on these three configurations. After the task, the experimenter covertly observed the participants who were left alone in a lab room and measured how long the participants voluntarily worked on the new set of puzzles left in the same room. This voluntary engagement in the task during this period was used as the index of intrinsic motivation. The results showed that participants in the choice condition were voluntarily engaged with the puzzle significantly longer than those in the forced-choice condition, suggesting that providing personal choice would enhance people's intrinsic motivation. In another study, the effects of personal choice were examined in educational contexts with elementary schoolchildren (Cordova & Lepper, 1996). Participants played with educational computer activities in which they can learn the topic of arithmetical order-of-operations. Participants in the choice condition were allowed to change instructionally irrelevant features of the program, such as the specific icons representing the child and the computer, whereas participants in the forced-choice condition were not. The results showed that personal choice facilitated students' intrinsic motivation as well as task performance.

How does personal choice facilitate people's motivation and performance? Some neuroscientific studies provided clues to this question. In Legault and Inzlicht (2013)'s study using electroencephalography (EEG), participants performed a Stroop task, where they were presented with a series of colored words and asked to identify the color of the ink with which the word is printed (e.g., the word BLUE printed in red ink). Before the task, participants in the choice condition read a descriptive list of four computer tasks and were asked to select one computer game that they wanted to play the most. Actually, these tasks described the Stroop task in different ways and participants were directed to the same Stroop task regardless of their choices. Participants in the forced-choice condition, on the other hand, saw the same list of the task descriptions but were pressured to select a specific task that the experimenter suggested. Consistent with the previous findings, providing personal choice of the task improved the task performance of the Stroop task (i.e., error rate of the trials where the color of the ink and the presented word are incongruent).

More importantly, the authors also examined the effects of personal choice on error-related negativity (ERN), which is characterized as a pronounced negative deflection on EEG signal that occurs within 100 ms of making an error on a task. Previous studies have suggested that the ERN reflects an error detection system (presumably located in the ACC) that monitors performance (Holroyd & Coles, 2002). Some other studies provided a complementary view, indicating that ERN reflects motivational and affective responses to errors (Hajcak & Foti, 2008; Luu, Collins, & Tucker, 2000). From both perspectives, ERN is considered critical to improve task performance. The authors found that participants in the choice condition showed a greater magnitude of the ERN than the participants in the forced-choice condition, and also that an increased magnitude of the ERN mediated the relationship between choice manipulation and improved task performance. These results suggest that personal choice enhanced task performance by increasing task monitoring or motivational responses after failure. In fact, participants in the choice condition showed slower reaction time after failure, which possibly reflects behavioral adjustments to reduce further errors.

These findings indicate the critical role of failure feedback processing to understand the facilitative effects of personal choice in motivation and performance. This idea is also supported by a recent neuroimaging study. In Murayama et al.'s (2015) experiment, which used fMRI, participants played with a game-like task called "stopwatch task." For each trial, they could decide the design of the stopwatch that they would play with, but participants were also explicitly told that the design of the stopwatch was nothing to do with task difficulty (i.e., the choice of appearance would in no way, directly influence task performance). Participants completed the task in two types of trials. In choice trials, participants could freely choose the design of stopwatch that they would play with. In forced-choice trials, participants were forced to choose a specific design which was suggested by a computer. Corroborating the previous findings, task performance was enhanced when participants were provided with personal choice as compared to forced-choice. Importantly, they also found that this enhanced task performance in the choice trials was related to the failure feedback processing in the brain. When negative feedback about the task was delivered, the vmPFC showed decreased activation (in comparison to the success feedback) in the forced-choice trials (Fig. 3). This pattern is consistent with the past neuroscientific literature, indicating that negative feedback serves as an aversive outcome (Hare, O'doherty, Camerer, Schultz, & Rangel, 2008; Noonan, Mars, & Rushworth, 2011). In the choice condition, however, this decrease in the vmPFC activation was not observed. In other words, negative feedback was no longer aversive in the choice trials. The authors interpreted these findings as people offsetting the negative emotional value of failure, by treating the feedback informationally and thus embracing the positive experience of using the feedback on their own behalf. It is also worth mentioning that the striatum, another key brain structure in the reward network, did not show this pattern of activation, indicating that the vmPFC and the striatum may play different roles in doing the task (for another interesting dissociation between the striatum and the vmPFC in response to negative feedback, see Bhanji & Delgado, 2014).

A related, but different line of classical research in cognitive psychology revealed the beneficial effects of personal choice on memory performance (Monty & Permuter, 1975; Monty, Rosenberger, & Perlmuter, 1973; Perlmuter, Monty, & Kimble, 1971; Perlmuter, Scharff, Karsh, & Monty, 1980; Takahashi, 1992). In these experiments, participants are typically presented with cue-target word pairs, but unlike standard memory experiments, there are multiple (typically five) cues or targets. In choice conditions,

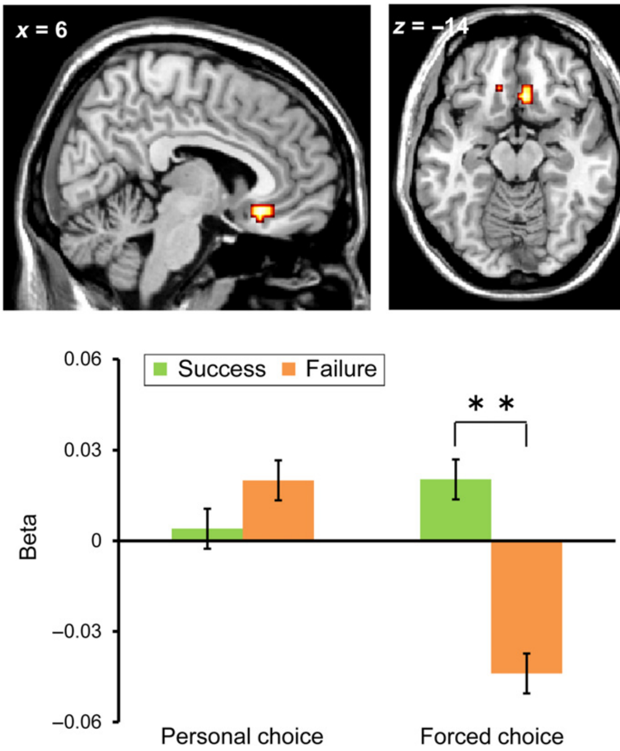

Fig. *3*. Right vmPFC Activation Showing a Significant Choice Condition by Outcome Valence Interaction in Response to Task Feedback as Reported by Murayama et al. (2015). *Notes*: In response to success feedback, the vmPFC activation in the self-determined-choice (i.e., personal choice) condition was not different from that in the forced-choice condition. On the other hand, the self-determined-choice condition showed higher vmPFC activation as compared to the forced-choice condition in response to failure feedback.

they can select one target (when multiple targets are presented) and the selected cue-target word pairs are presented in the subsequent learning phase. In forced-choice conditions, a specific target word is assigned by the experimenter, and these assigned cue-target word pairs are presented in the subsequent learning phase. Findings from these studies repeatedly showed that memory performance would be enhanced for the word pairs for which participants had opportunity to select cues or targets (Monty et al., 1973; Perlmuter et al., 1971). It is worth noting that the effect of personal choice on memory performance seems to be stronger after a 24-hour delay, rather than in immediate tests (Monty & Permuter, 1975).

Studies in cognitive neuroscience (Lisman & Grace, 2005; Shohamy & Adcock, 2010) have revealed that activation in the striatum (i.e., part of the reward network) facilitates declarative memory by modulating the activation in the hippocampus (i.e., memory system in the brain). In fact, several studies demonstrated that the provision of extrinsic rewards (e.g., money) can enhance memory performance, especially after a long delay (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Wittmann et al., 2005). As described earlier, several studies showed that personal choice can also activate the reward network in the brain (Aoki et al., 2014; Fujiwara et al., 2013; Leotti & Delgado, 2014; Leotti et al., 2010), indicating that choice has a rewarding property. Then, we can hypothesize that choice enhances memory performance through the modulation of the striatum into the hippocampal memory system. A recent study by Murty, Dubrow, and Davachi (2015) directly tested this hypothesis using fMRI. These studies found that the striatal activation in response to choice opportunity cue indeed predicted memory performance after 24-hours delay in choice condition, and that the coupling activation between the striatum and the hippocampus was observed only for the items that participants correctly remembered. These findings indicate that personal choice facilitates memory performance in a different way, as it enhances the performance of tasks that requires feedback learning.

PUTTING IT ALL TOGETHER: INTEGRATING THE PSYCHOLOGICAL EXPERIENCE AND BEHAVIORAL ACT OF PERSONAL CHOICE WITH NEUROSCIENTIFIC EVIDENCE AND EXPLANATIONS

Our literature review showed that the mere act of making a personal choice would involve a variety of psychological processes, and the emergent body of the neuroscientific literature indicated that these choice effects are supported by several distinct brain areas. One of the key brain areas that repeatedly emerged in our literature review was the striatum. The striatum is activated when people expect choice opportunities (Aoki et al., 2014; Fujiwara et al., 2013; Leotti & Delgado, 2011, 2014; Murayama et al., 2015), and choice-induced preference change manifests as the increased activation in this brain area for the items that participants chose. These observations indicate that some of the choice effects may be parsimoniously explained by a broader, reward process in the brain (see also Hidi, 2015). For example, although different researchers proposed different psychological mechanisms to explain the facilitative effects of personal choice on memory performance (e.g., multiple-cues hypothesis; see Toyota, 2013), memory consolidation caused by the reward processing in the brain (Shohamy & Adcock, 2010) would provide a simple but more powerful and clearer explanation for the past findings (Murty et al., 2015).

The vmPFC, a different brain area that also constitutes the reward network, involves choice effect as well, but this area seems to play a more nuanced role. In fact, in the papers that we reviewed, the activation of the vmPFC is consistently modulated by task context or social environment, whereas the activation of the striatum is not. For example, Aoki et al. (2014) showed that the striatum was responsive to the number of choice opportunities, but the vmPFC was more sensitive to the social comparison of these choice opportunities. Murayama et al. (2015) also found that the choice effects modulate the feedback processes in the vmPFC, but not in the striatum. Kool et al. (2013) reported the insensitivity of the striatum activation to a contextual factor (i.e., illusion of control). Both the striatum and the vmPFC have been strongly implicated in reward-related processing in the brain (Haber & Knutson, 2010), but their functional dissociation has not been well documented in the literature, except for relatively few cases (Hare et al., 2008; Knutson, Fong, Adams, Varner, & Hommer, 2001). We speculate that, in contrast to the vmPFC, the striatum may entail crude and automatic valuation processes that are relatively insensitive to the context. This idea actually corroborates the large body of literature in psychology, proposing that the human evaluation process is supported by two qualitatively different systems – an automatic, general process and an elaborative, context-specific process (dual-process model; Cacioppo & Petty, 1985; Kahneman, 2003). This dichotomy may also be related to the distinction between model-free and model-based mechanisms in reinforcement learning, which has attracted recent attention in decision neuroscience (Daw et al., 2011; O'Doherty, 2012). It is possible that this distinction may map onto the functional dissociation between the striatum and the vmPFC especially in the context of choice effects (Murayama et al., 2015). Further research is needed to clarify the distinct roles of these brain regions in the psychological processing of personal choice.

Another brain area that seems to be important to understand the neural underpinning of personal choice is the pMFC (especially the dACC).

Cognitive dissonance induced by difficult choice was related to the pMFC activity (Izuma et al., 2010; Kitayama et al., 2013). Effects of personal choice were also mediated by the dACC activation, especially in relation to the processing of negative feedback (Legault & Inzlicht, 2013). The activation of the dACC was observed in response to (unsigned) prediction error signals when the illusion of control was induced (Kool et al., 2013). Personal choice also alleviated the activation of the dACC in response to painful stimuli (Salomons et al., 2004). One interesting feature of the pMFC is that, unlike the vmPFC, the pMFC receives strong projections from motor-related areas such as the primary motor cortex and the supplementary motor area, suggesting that part of the effects of personal choice may be mediated by motor-related signals (consistent with the idea of embodied motivation; e.g., Zhang & Risen, 2014). However, given that the dACC has been implicated in various psychological functioning, including conflict monitoring (Botvinick, Cohen, & Carter, 2004) and outcome saliency (Litt, Plassmann, Shiv, & Rangel, 2011), we do not believe it is appropriate to provide a single general account of how the pMFC or dACC plays a role in different experimental paradigms involving personal choice. Rather, the role of this brain area in studies of personal choice should be discussed on an individual basis, taking into account experimental contexts and psychological mechanisms that are specific to each study.

AUTONOMY NEUROSCIENCE

These studies are clearly still at a nascent stage, but the accumulating evidence we reviewed above shows some consistent pattern of findings, which indicates the importance of studying the topic in a more systematic and integrative manner. To facilitate the interactions and the integrity of the past and future research programs, we suggest that research be conducted as a new realm in social and cognitive neuroscience, which we shall call "autonomy neuroscience." As emerged from our literature review, autonomy neuroscience is an interdisciplinary field devoted to the neuroscientific understanding of how and why our autonomous decision making (as opposed to controlled or forced decision making) motivates our behavior. Autonomy neuroscience is different from decision neuroscience – one of the most popular realms in cognitive neuroscience – in that decision neuroscience is concerned only with the factors that make people adopt (or avoid) specific choices (e.g., value, cost, prediction error), but not with the distinction between autonomous decision making (e.g., personal choices) and controlled decision making (e.g., forced-choices). Autonomy neuroscience is also different from the large body of literature on the neuroscience of consciousness and free will (e.g., Haggard, 2008). This line of research examines the neural mechanisms underlying the consciousness or agency itself, but does not address the motivational aspects of autonomous behavior. In short, autonomy neuroscience addresses how and why "your" choice motivates you in the brain.

It should be noted that we do not argue that the "active-agent" or "autonomous" view of human behavior is unequivocally correct. In fact, recent research in cognitive science has revealed that our decision-making process is not always mediated by active, willful cognitive processing (Haggard, 2008; Johansson, Hall, Sikstrom, & Olsson, 2005; Shimojo, Simion, Shimojo, & Scheier, 2003; Wegner, 2003). Many of these studies showed that our decisions are sometimes determined prior to when we feel we made a choice, suggesting that our sense of agency or autonomy may not play a critical role in our choices. However, regardless of whether our choices are real or not, it is possible that (the sense of) personal choice and forced-choice would elicit different psychological and motivational processes. The question of whether we are autonomous or have free will and the question of whether the sense of autonomy or personal choice motivates people are separate issues.

ADDITIONAL CONSIDERATIONS

Several remarks should be noted. First, to provide rigorous neuroscientific evidence about the effect of personal choice, there is one inherent methodological challenge that we need to bear in mind — an item selection effect. For example, when we compare choice and forced-choice conditions, participants in the choice condition can choose the items that they like, and participants in the forced-choice condition are typically assigned to the items that are yoked to the choice made by the participants in the choice condition. This means that participants in the forced-choice condition may be assigned to the items that they do not like. Therefore, the comparison between the choice condition and the forced-choice condition confounds the effect of personal choice with the effects of pre-existing (or momentary) personal preferences. In other words, as long as we let participants choose what they want, we cannot randomly assign stimuli or tasks between choice and forced-choice conditions, and therefore, we cannot make causal inference in a strict manner. This issue is essentially the same with the criticism raised by Chen and Risen (2010) on choice-induced preference change. In our literature review, only a limited number of studies explicitly noted and addressed this issue of item selection bias (e.g., Izuma et al., 2010; Murayama et al., 2015). To understand the precise neural mechanisms underlying choice, future research, especially the studies that compare choice and forced-choice (or no choice) conditions, should attend more closely to this methodological issue.

Second, all of the neuroscientific studies we reviewed focused on the positive aspects of personal choice, but personal choice does not always benefit people. One of the most popular examples of a negative aspect of personal choice is choice overload (Iyengar & Lepper, 2000). Choice overload is a phenomenon where people have difficulty in making a decision when they are faced with too many options. In one study (Iyengar & Lepper, 2000), participants were provided with the opportunity to make a selection from a limited array (6) or an extensive array (30) of chocolates. Participants in the extensive choice condition (in comparison to the limited choice condition) found the choice more enjoyable but frustrating, and importantly exhibited more dissatisfaction and regret about their choices (but see also Chernev, Böckenholt, & Goodman, 2015; Simonsohn, Nelson, & Simmons, 2014; which question the robustness of the findings). These results indicate that, although increased number of choice options would produce increased rewarding value (Aoki et al., 2014; Fujiwara et al., 2013; Suzuki, 2000), having too many options does not always bring adaptive psychological consequences.

Similarly, choice may be rewarding, but this does not necessarily mean that personal choice always brings benefits to the agent. This would sometimes create a paradoxical situation where people prefer the freedom to choose based on the belief that such freedom would allow them to maximize the positive outcome, but such preference inadvertently diminishes positive outcomes. In social psychology, for example, researchers found that people tend to prefer the freedom to choose even though such freedom would actually prevent people's reappraisal process about the decision, resulting in reduced well-being. Gilbert and Ebert (2002) asked students to enroll in an extracurricular photography class. In the class, the students took photographs and selected their two favorite photographs. Then students were asked to pick one of the photographs to keep for themselves and to donate the other to the school. Before making their decision, half of the students were told their choice was final and the other half were told they would have several days to contemplate their choice and exchange the photograph if they so desired. There are many situations like this in our daily life (e.g., you have an option of returning an item that you purchased if you do not like that). You may think that it would be good to have the option of exchanging the photograph later, as this would give you a more flexible choice. However, it turned out that those who were allowed to exchange it were less pleased with their selection than those who were forced to finalize the selection. This is because being committed to a specific option would make people engage in the psychological reappraisal process that justifies the choice of the option (this is a similar process with choice-induced preference change).

As another example, in the realm of self-regulated learning in cognitive psychology, there are many instances where people tend to choose study strategies that they believe to beneficial but they are actually suboptimal, especially for long-term learning (Bjork, Dunlosky, & Kornell, 2013). In some cases, providing a forced-choice of study strategies would benefit learning more than providing participants with the complete freedom to select study strategies (Kornell & Bjork, 2008; Murayama, Blake, Kerr, & Castel, in press). In sum, these ironic consequences of personal choice have not received a great deal of attention in the neuroscience literature, and may merit future inquiry.

Third, and relatedly, although our chapter may have implied that choice is generally motivationally beneficial, the effects of choice should be considered with context. In fact, research in educational psychology has often found that choice is motivating only when the choice is meaningful and valuable to people (Katz & Assor, 2007). For example, a study showed that the provision of choice did not facilitate motivation when choice has to be made among mandated options (Reeve, Nix, & Hamm, 2003). Providing choice options would be easy to implement in many practical settings such as education. But given that choice can take myriad of different forms in real-life settings, and not all the choices are equally beneficial, we need to be careful to translate research findings into practical contexts.

Fourth, the question of why people feel value for the freedom of choice would also merit future inquiry. Some researchers argue that people's preference for choice has been adaptively selected for evolutionary survival and that we have an innate tendency to seek the freedom of choice (Leotti et al., 2010). However, it is also possible that personal choice would on average allow people to receive more rewards in their life history, and therefore the preference for choice may simply reflect individual's reinforcement history. This perspective can also explain why there are large individual differences in our preference for choice (Rotter, 1966). In addition, there are several studies that showed the cultural influences on the functionality and the value of personal choice (Iyengar & Lepper, 1999; Savani, Markus, & Conner, 2008), indicating the importance of social environment. These two possibilities are not mutually exclusive, but unfortunately, none of the current behavioral, neuroimaging, or animal studies can directly answer the question of whether, and to what extent, people have the inborn tendency to value personal choice. A broader approach such as developmental examination or behavioral genetics would be a good future avenue to address this question.

CONCLUSION

In his very influential paper published in 1977, Albert Bandura proposed that people strive and are able to exercise control over events that affect their lives – people are "active agents" that enjoy their own choices to change outcomes and environments (Bandura, 1977). A similar proposal was made by Deci and Ryan (1985), who claimed that humans are naturally inclined to make personal choices and actively interact with the environment to satisfy the basic need for autonomy. The idea that we value our own choice and autonomy excited a number of researchers in psychology, and indeed, it set a foundation for the contemporary theories on motivation. But this enthusiasm has not apparently been shared by researchers in neuroscience; as indicated in the introduction, behavioristic views on motivation has overshadowed potential motivating quality and value of personal choice (as opposed to forced-choice). The current chapter reviews this sparse, but emergent, body of neuroscientific literature to address possible neural correlates underlying personal choice, especially focusing on the following motivational aspects – (i) personal choice is rewarding, (ii) personal choice shapes preference, (iii) personal choice changes the perception of outcomes, and (iv) personal choice facilitates motivation and performance. The evidence is not conclusive, but we hope that this review would leverage more extensive neuroscientific work on personal choice, and more broadly, contribute to the future prospect of "autonomy neuroscience."

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INSULAR CORTEX ACTIVITY AS THE NEURAL BASE OF INTRINSIC MOTIVATION

Woogul Lee

ABSTRACT

Many psychologists posit that intrinsic motivation generated by personal interest and spontaneous satisfactions is qualitatively different from extrinsic motivation generated by external rewards. However, the contemporary neural understanding of human motivation has been developed almost exclusively based on the neural mechanisms of extrinsic motivation. In neuroscience studies on extrinsic motivation, striatum activity has been consistently observed as the core neural system related to human motivation. Recently, a few studies have started examining the neural system behind intrinsic motivation. Though these studies have found that striatum activity is crucial for the generation of intrinsic motivation, the unique neural basis of intrinsic motivation has not yet been fully identified. I suggest that insular cortex activity, known to be related to intrinsic enjoyment and satisfaction, is a unique neural component of intrinsic motivation. In this chapter, I addressed the theoretical background to and empirical evidence for this postulation.

Keywords: Intrinsic motivation; self-determination theory; curiosity; competence; insular cortex; striatum

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People may study to gain a full scholarship, or they may study because they just enjoy studying. In other words, motivation may arise from both extrinsic (e.g., rewards, bonus scores, and good grades) and intrinsic reasons (e.g., interest, enjoyment, and curiosity). Individuals are sometimes motivated into action because they expect that what they do will produce external reinforcement; other times, they are motivated into action because they expect intrinsic satisfaction. Motivation researchers in the field of psychology call the former extrinsic motivation and the latter intrinsic motivation, and distinguish one from the other (Deci & Ryan, 1985; Ryan & Deci, 2000).

Previous research findings in psychology support the idea that intrinsic motivation is qualitatively different from extrinsic motivation. It is thought that intrinsic motivation arising from curiosity, interest, autonomy, or competence is more beneficial for human functioning (e.g., creativity, depth of engagement, conceptual understanding of what one is trying to learn, and psychological well-being) than is extrinsic motivation, which arises from the anticipation of beneficial consequences (Amabile, 1985; Cordova & Lepper, 1996; Reeve, Jang, Carrell, Jeon, & Barch, 2004; Sheldon, Ryan, & Reis, 1996; Vansteenkiste, Simons, Lens, Soenens, & Matos, 2005). Results also suggest that these two types of motivation do not have synergic effects on human functioning when they are provided simultaneously. This means that, if extrinsic rewards are provided when people engage in an activity for which they would naturally be intrinsically motivated, intrinsic motivation can be undermined once the extrinsic rewards are taken away (Deci, 1971; Deci, Koestner, & Ryan, 1999; Lepper, Greene, & Nisbett, 1973).

TRADITIONAL NEUROSCIENTIFIC PERSPECTIVES ON HUMAN MOTIVATION

Whereas intrinsic motivation is commonly accepted to be an important type of motivation in psychology, neuroscience research on human motivation traditionally tends to focus exclusively on extrinsic motivation (Berridge, 2004; Cardinal, Parkinson, Hall, & Everitt, 2002; Robbins & Everitt, 1996). This is consistent with the basic behaviorist approach in which human motivation can be understood by the effect of attractive external rewards (e.g., food, drinks, and money) that can change human behavior in a direct and visible way. To understand the contemporary neural understanding of human motivation, it is important to review the current neuroscientific knowledge of extrinsic motivation.

NEURAL FINDINGS FROM ANIMAL STUDIES

In the field of neuroscience, many assumptions regarding human motivation have been traditionally based on the reactions of animals toward extrinsic rewards (Cardinal et al., 2002; Mogenson, Jones, & Yim, 1980; Schultz, 2000). This tradition might be due to the limitations of neuroscientific methods on human beings in the past and the assumption that the basic neural mechanism of motivation is quite similar between animals and human beings.

Physiological needs produce motivated behavior in reaction to need-satisfying incentives. When animals have physiological needs like hunger and thirst, those needs lead them to search for food and drink. They then experience physiological need satisfaction when food and drink are ingested. As need-satisfying experiences are accumulated, the animals can learn the incentive value and satisfying-potential of various sources of sustenance. Through this process, need-satisfying incentives (e.g., food and drink) come to act as extrinsic (environmental) sources of motivation.

Neuroscience researchers have tried to understand the neural processes of motivation by investigating which brain regions play an important role and how the neural activity of these brain regions change. According to previous findings from animal studies (Cardinal et al., 2002; Robbins & Everitt, 1996; Schultz, 2000), the key neural systems in the initiation of biologically significant behavior for extrinsic rewards include the activations of the striatum (e.g., the nucleus accumbens, caudate, and putamen), the limbic system (e.g., the amygdala and thalamus), the prefrontal cortex (e.g., the orbitofrontal cortex), and the motor system (e.g., the supplementary motor area and pre-supplementary motor area). In particular, researchers have emphasized the functional role of the striatum in motivation because motivated behavior is closely related to dopamine increases in the striatum. The pursuit of extrinsic rewards activates dopamine neurons in the striatum, which initiates the actions required to acquire these extrinsic rewards (Berridge & Robinson, 2003).

NEURAL FINDINGS FROM HUMAN NEUROIMAGING STUDIES

In recent decades, as neuroimaging methods have been advanced, numerous studies targeting human subjects have been conducted. Researchers have sought to identify the neural system of human motivation by observing neural activity at the moment when extrinsic rewards are expected or received. According to previous findings (McClure, York, & Montague, 2004; O'Doherty, 2004; Smith & Delgado, 2015), the neural correlates of reward processing, such as striatum activity and orbitofrontal cortex activity, are the core neural mechanism of human motivation. These neural findings from human neuroimaging studies are consistent with those from animal studies.

Early human motivation research generally used primary rewards such as food, fruit juice, and water as the basis for experimentation, while more recent research has expanded the range to social and conditional rewards such as money, esthetic preferences, positive feedback, and positive social interaction (Izuma, Saito, & Sadato, 2008; Kirsch et al., 2003; Lacey et al., 2011; Lee & Kim, 2014). Results of these studies have demonstrated that the brain regions related to reward processing (e.g., striatum, limbic area, and prefrontal cortex) are commonly activated not only by primary rewards but also by conditional or social rewards. For instance, Izuma et al. (2008) found that the striatum (e.g., caudate and putamen), known as a key brain region for reward processing, was commonly activated not only when people received tangible monetary rewards but also when they received social rewards (e.g., positive impression evaluations). These results suggest that, regardless of motivation type and modality, the traditional motivation theories derived from animal studies are applicable to human beings.

However, one notable difference between animals and humans is that, in motivational processes, prefrontal areas are relatively more important to the latter. In particular, the orbitofrontal cortex has been identified as a core area of neural activity with regards to human motivation. The orbitofrontal cortex represents the value of rewards, regardless of their type, in terms of a "common currency." Due to this, the relative value of different rewards (e.g., primary, social, or conditional rewards) can be compared on a single scale (Kringelbach & Rolls, 2004; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Rolls, 2000).

INTRINSIC MOTIVATION RESEARCHERS' INTEREST IN NEUROSCIENTIFIC APPROACHES

Intrinsic motivation researchers in psychology have recently started showing interest in neuroscientific methods (Legault & Inzlicht, 2012;

Murayama, Matsumoto, Izuma, & Matsumoto, 2010; Murayama et al., 2015; Reeve & Lee, 2012). This is because traditional methods used to measure intrinsic motivation have some limitations which have been criticized by researchers against the concept of intrinsic motivation (Cameron & Pierce, 1994; Eisenberger & Cameron, 1996; Locke & Henne, 1986). For example, in the case of behavioral measures, researchers may leave participants alone in the experimental room after completing an interesting experimental task in order to see if they voluntarily engage and persist in the same task during this free time (Deci, 1971). However, this behavioral measure is not direct evidence of intrinsic motivation but rather indirect evidence showing observable consequences of intrinsic motivation (e.g., persistence). This means that the results of this behavioral measure can be influenced not only by intrinsic motivation but also by other factors (e.g., preparing for future trials).

Self-reported measures (e.g., Intrinsic Motivation Inventory) have also been widely used in order to measure intrinsic motivation (Plant & Ryan, 1985; Ryan, Mims, & Koestner, 1983), but the self-reported measures have the following limitations. First, these measures may not accurately capture the dynamic aspect of intrinsic motivation. This is because participants are not usually able to respond at the moment of experiencing intrinsic motivation. Rather, participants are likely to respond based on their memory after experiencing intrinsic motivation. Second, participants' self-reported responses can be biased intentionally or unintentionally. Social desirability can influence participants' self-reported responses when self-reported measures of intrinsic motivation include items with socially favorable words or situations (Edwards, 1957). Or, participants' responses can be inaccurate because they cannot perceive nonconscious aspects of intrinsic motivation such as priming (Schultheiss, 2008).

Many researchers believe that these neuroscientific methods can partially compensate for the limitations of traditional intrinsic motivation measures and contribute to theoretical advances in intrinsic motivation research. Of course, neuroscientific methods have their own limitations. In functional magnetic resonance imaging studies, for instance, intrinsic motivation is measured in an artificial way (i.e., lying in a scanner when performing tasks). However, despite these limitations, neuroscientific methods can capture the basis of intrinsic motivation on a microscopic scale, the implicit aspects of intrinsic motivation, and on-going changes in intrinsic motivation. Though neuroscience-based motivation theories are generally based on the neural mechanisms of extrinsic motivation (Berridge, 2004), psychology-based motivation theories argue that intrinsic motivation is qualitatively different from extrinsic motivation (Reeve & Lee, 2012; Ryan & Deci, 2000). In line with this psychology-based approach, researchers have thus started conducting empirical studies on intrinsic motivation applying neuroscientific methods.

RECENT NEUROSCIENTIFIC FINDINGS ABOUT INTRINSIC MOTIVATION

Intrinsic motivation refers to the inherent propensity to pursue one's interests, to seek out novelty and challenges, to satisfy curiosity and competence, and to extend one's capacities (Deci & Ryan, 1985; Reeve, 2015). Neuroscience studies on intrinsic motivation are rare partly because intrinsic motivation can be more difficult to generate in neuroscience experiments compared to extrinsic motivation. As discuss in the previous section, extrinsic motivation can be easily and reliably manipulated by providing attractive extrinsic rewards or by causing the participants to expect those extrinsic rewards. In contrast, the manipulation of intrinsic motivation can be relatively complicated (e.g., setting up situations that lead participants to experience a sense of competence). Therefore, we need to understand the detailed experimental procedures used in neuroscience studies on intrinsic motivation. In recent neuroscience studies, intrinsic motivation has been manipulated in various ways by tapping the well-known underlying sources of intrinsic motivation (e.g., competence and curiosity).

Neuroscience Studies on Intrinsic Motivation

Competence

Competence is a need that energizes one's willingness to seek out and master optimal challenges (Deci & Ryan, 1985). Some neuroscience studies have examined the neural correlates of intrinsic motivation by manipulating participants to experience either high or low levels of competence (Mizuno et al., 2008; Murayama et al., 2010). In the study of Mizuno et al. (2008), for example, participants performed a working memory task (i.e., an *n*-back task) and received academic feedback on whether their answers were correct or not. With this experimental paradigm, the neural correlates of intrinsic motivation were examined as measuring neural signal changes when participants received positive academic feedback and, as a result, experienced a sense of competence. Of the several brain regions activated as a consequence of intrinsic motivation, the authors paid attention to the putamen, a part of the striatum, because its activations were significantly correlated with participants' self-reported intrinsic academic motivation. Based on these results, the authors insisted that striatum activity, particularly that of the putamen, plays an important role in the neural system of intrinsic motivation.

Curiosity

Curiosity is a need that energizes one's willingness to seek out novelty and to solve the mystery (Deci & Ryan, 1985). The neural mechanisms of intrinsic motivation have also been examined by manipulating the levels of curiosity satisfaction in participants (Gruber, Gelman, & Ranganath, 2014; Kang et al., 2009). Kang et al. (2009) examined neural activity when participants read trivia questions and thought of the correct answers before they were provided, which stimulates feelings of curiosity. It was found that the caudate, which is also a part of the striatum, and the lateral prefrontal cortex were activated when participants experienced curiosity and subsequent satisfaction. Furthermore, these results neurally and behavioral confirmed that increased neural activations related to curiosity led to an improvement in the memory of the participants. In a similar study, Gruber et al. (2014) also investigated the neural mechanisms of curiosity. Results also demonstrated that the activations of the striatum and the midbrain dopaminergic pathway, including the substantianigra and ventral tegmental area, were closely related to curiosity. The mean recall test score for curiosity-inducing questions was also higher than that for the control questions, which also confirmed the beneficial effects of curiosity on memory enhancement.

Undermining Effects of Extrinsic Rewards on Intrinsic Motivation

Murayama et al. (2010) sought to find neural evidence supporting the psychological hypothesis that extrinsic rewards undermine the effects of intrinsic motivation (Deci, 1971; Lepper et al., 1973). In their experiment, the influences of extrinsic rewards on the neural system of intrinsic motivation were examined by comparing the neural activations when (a) participants performed an interesting task (i.e., a stopwatch task; Time 1), (b) participants performed the same interesting task and received monetary rewards contingent upon their performance (Time 2), and (c) participants performed the same interesting task without monetary rewards (Time 3). Participants were manipulated to experience intrinsic motivation when performing the interesting task and receiving competence feedback (i.e., positive feedback). The results showed that the caudate was activated when participants only experienced intrinsic motivation (Time 1) and also when they received extrinsic rewards during the performance of the interesting task (Time 2). However, caudate activity weakened when the extrinsic rewards were subsequently withheld during the performance of the interesting task (Time 3). These results suggest that striatum activity, particularly that of the caudate, plays an important role in the neural systems of both intrinsic and extrinsic motivation. Furthermore, neural changes in the caudate (from Time 1 to Time 3) confirmed the human motivation hypothesis that extrinsic rewards can undermine the effects of intrinsic motivation.

Implications and Limitations

These aforementioned findings suggest that the neural mechanisms of reward processing play an important role in the neural systems of both intrinsic and extrinsic motivation. It implies that there is a common neural mechanism of motivation regardless of whether the underlying source is internal (i.e., intrinsic motivation) or external (i.e., extrinsic motivation) (Braver et al., 2014; Gruber et al., 2014). This suggestion is in line with the recent neuroscientific consensus that the neural mechanisms of reward processing operate regardless of the type of reward, be it primary (e.g., food and drink), secondary (e.g., money), or social (e.g., positive social interaction) (Izuma et al., 2008; Kirsch et al., 2003). These neuroscience studies also confirm that intrinsic motivation has beneficial effects on learning, such as memory enhancement, self-regulation, and resilience in the face of failure (Gruber et al., 2014; Kang et al., 2009; Lee & Kim, 2014; Legault & Inzlicht, 2012; Murayama et al., 2015).

However, remaining issues still exist. Even though neuroscience research has established the undermining effect of extrinsic rewards on intrinsic motivation, which indirectly supports the qualitative difference between intrinsic and extrinsic motivation (Murayama et al., 2010), there is little direct neural evidence. Of course, many studies have demonstrated that neural circuits related to reward processing are commonly recruited when people are both intrinsically and extrinsically motivated. These results suggest that the neural basis of intrinsic motivation is similar to that of extrinsic motivation. However, the other possibility is that neuroscience researchers have disregarded areas of neural activity outside those involved in reward processing. This is possible because the brain regions related to reward processing have been treated as Regions of Interest (ROIs) within the framework of the traditional neuroscientific approaches about human motivation. For example, the neural activations of the insular cortex, which may be uniquely related to intrinsic motivation and will be discussed further in the following section, were also observed in other studies about intrinsic motivation (Mizuno et al., 2008; Murayama et al., 2015); however, insular cortex activity has not received close attention until very recently.

NEW PERSPECTIVES ON THE NEURAL MECHANISMS OF INTRINSIC MOTIVATION

Neural Differences between Intrinsic and Extrinsic Motivation

My colleagues and I have attempted to investigate whether the neural system of intrinsic motivation is qualitatively different from that of extrinsic motivation. To do so, we have conducted several neuroscience studies capturing unique underlying neural mechanisms of intrinsic motivation by comparing the neural activations of intrinsic and extrinsic motivation. In these studies (Lee & Reeve, 2013; Lee, Reeve, Xue, & Xiong, 2012), we compared neural activations when participants imagined a situation in which they were engaged in intrinsically motivating activity to neural activations when they imagined engaging in the same activity except for an extrinsically motivating reason. For example, the former condition encouraged the participants to think of a time when they were working on the computer out of curiosity, whereas the latter condition encouraged them to think of a time when they participated in computer work for bonus points (Fig. 1).

It was found that the anterior region of the insular cortex showed greater activations when the participants imagined an intrinsically motivating situation than when they imagined an extrinsically motivating one. These results inspired us to think about the fundamental differences in the underlying mechanisms of motivation depending on whether the motivation derived from an internal or external source. In particular, we found a positive correlation between participants' self-reported intrinsic satisfaction and the neural activations of the anterior insular cortex when the participants imagined an intrinsically motivating situation (Lee & Reeve, 2013). This suggests that neural activity within the anterior insular cortex is a unique component of the neural mechanism of intrinsic motivation (Fig. 2).

The neural activations of the anterior insular cortex when the participants thought about an intrinsically motivating situation are particularly interesting. According to many other neuroscientific findings (Craig, 2009; Morris, 2002), however, the insular cortex rarely engages in the initiation of motivated behavior. Therefore, even though the anterior insular cortex plays an important role in intrinsic motivation, it is difficult to conclude that the neural activations of the anterior insular cortex account for the entire intrinsic motivation process, including the initiation of motivated behavior. Indeed, in the field of neuroscience, the striatum is widely accepted to be the brain region that plays a major role in the generation of motivated behavior (Cardinal et al., 2002; McClure et al., 2004; Schultz, 2000).

There are two possible explanations why striatum activity was not observed in our research. The first explanation might be that the neural activations of intrinsic motivation occurred when the participants considered an intrinsically motivated situation, not when they actually experienced intrinsic motivation during task engagement. Previous neural findings about human agency indicate that imagining a particular behavior tends to produce brain activation patterns similar to those produced when actually engaged in that behavior (Decety, 1996; Ruby & Decety, 2001). However, imagining motivated behavior may still be insufficient to stimulate the exact state of intrinsic motivation which is conceptually assumed as an on-going state. Second, the neural findings of our previous studies might also be limited by the analysis method employed, which compared neural activations between two experimental conditions (i.e., intrinsic motivation vs. extrinsic motivation). By conducting this type of analysis, we could only identify neural differences between intrinsic and extrinsic motivation; the core neural mechanisms of motivational processes shared by intrinsic and extrinsic motivation (i.e., hypothesized striatal activity) may be left unexamined.

NEURAL DIFFERENCES BETWEEN HIGH VERSUS LOW LEVELS OF INTRINSIC MOTIVATION

Considering these limitations, Reeve and I recently examined the neural activations when participants actually experienced intrinsic motivation during task performance. In addition, we compared high versus low levels of intrinsic motivation, not comparing the two different types of motivation (i.e., intrinsic motivation vs. extrinsic motivation). To create experimental conditions under which intrinsic motivation could be measured, curiosity-inducing and competence-enabling tasks were used (Fig. 3). For instance, we expected participants to seek out a challenge, to try to master it for the sheer fun of it, to enjoy the experience of being challenged and making progress, and to earn a sense of "I can do it" during competence-enabling task performance.

These psychological processes of intrinsic motivation were confirmed by the neural findings of the experiment. We found that the neural activity of the anterior insular cortex was a key neural component of intrinsic motivation, consistent with our previous research (Lee & Reeve, 2013; Lee et al., 2012). In addition, the striatum showed greater activations when participants experienced high levels of intrinsic motivation than when they experienced low levels of intrinsic motivation, which confirms the hypothesis that the striatum plays a key role in the neural system of intrinsic motivation, as it does for extrinsic motivation (Braver et al., 2014; Gruber et al., 2014). Furthermore, we found that the functional connectivity between the activations of the anterior insular cortex and those of the striatum was greater when participants experienced high levels of intrinsic motivation than when they experienced low levels of intrinsic motivation. The neural activations of the anterior insular cortex and those of the striatum observed during the performance of intrinsically motivating tasks suggest that intrinsic enjoyment and satisfaction (i.e., anterior insular cortex activity) and reward processing (i.e., striatum activity) are both important in different ways in the neural system of intrinsic motivation. The functional connectivity results of this study also suggest that communication between these two brain regions generates

NEURAL UNDERSTANDING ABOUT INSULAR CORTEX ACTIVITY

What then is the functional role of insular cortex activity in the neural system of intrinsic motivation? Because few neuroscience researchers have emphasized the role of the anterior insular cortex in the neural system of intrinsic motivation, it is helpful to broadly review how other researchers have interpreted the neural activations of the insular cortex observed in research on different but somewhat similar psychological states. Historically, the functions of the insular cortex were largely unknown because the insular cortex is a medial part of the brain and, as a result, is difficult to be investigated with traditional neuroscience methods. As advanced neuroimaging techniques (e.g., functional magnetic resonance imaging) have become more widely used, however, numerous researchers have shown their interest in the functions of the insular cortex.

Insular Cortex, Emotion, and Feeling

The insular cortex is well known for the processing of emotion and feeling (Craig, 2009; Morris, 2002). Early studies emphasized the relationship between insular cortex activity and negative emotions or feelings such as disgust, sadness, fear, and anger (Critchley, Mathias, & Dolan, 2002; Wicker et al., 2003). However, researchers later found that the insular cortex also processes positive emotions such as happiness (Damasio et al., 2000; Lamm & Singer, 2010). From these findings, it has been suggested that the insular cortex plays an important role in the processing of emotion and feeling regardless of valence. In addition to the insular cortex, many brain regions (e.g., the hypothalamus, amygdala, striatum, orbitofrontal cortex, and anterior cingulate cortex) are also involved in the processing of emotion and feeling (Pessoa, 2008; Wager et al., 2008). Of these, the reason why many researchers have paid special attention to the insular cortex might be due to its unique function. Many researchers have proposed that there is a functional distinction between the insular cortex and the amygdala in the processing of emotion and feeling, with the amygdala building the initial association between emotional stimuli and automatic responses and the insular cortex integrating emotionally salient information and forming subjective emotional feelings based on this information (Critchley et al., 2002; Morris, 2002).

The somatic marker hypothesis views the functional role of the insular cortex in a similar way (Bechara & Damasio, 2005; Damasio, 2003). This hypothesis emphasizes that people's emotion and feeling are important in the decision-making processes. According to the hypothesis, emotional stimuli or situations activate internal reactions (i.e., bodily responses), and emotion is generated based on the representations of these physical reactions. Based on the accumulated experience of bodily responses to emotional stimuli or situations, human beings can build subjective and conscious feelings about emotional stimuli or situations. At that time, the insular cortex represents conscious feelings based on accumulated information about emotional stimuli or situations, whereas the amygdala and the ventromedial prefrontal cortex, including the orbitofrontal cortex, help trigger the manifestation of particular bodily states.

Insular Cortex, Craving, and Addiction

Neural findings about craving and addiction have implications for understanding the neural system of intrinsic motivation. According to the neural findings about addiction, the key neural substrates of reward processing (e.g., the striatum and orbitofrontal cortex) are also related to craving and addiction, aggressive and excessive forms of motivation to drugs, drinks, or cigarettes (Kelley & Berridge, 2002; Schultz, 2000). This means that the expectations of pleasure (or hedonic rewards) from taking drugs, drinking, or smoking can lead people to addicted behavior.

Recent neuroscience studies about addiction have additionally emphasized the role of the insular cortex, which integrates the cognitive and emotional information regarding the substances that are the focus of the addiction (Brass & Haggard, 2010; Brody et al., 2002; Goldstein et al., 2009; Pelchat, Johnson, Chan, Valdez, & Ragland, 2004). In particular, Naqvi, Rudrauf, Damasio, and Bechara (2007) found that cigarette smokers ceased their addicted behavior after suffering insular cortex damage. One such participant made the intriguing statement, "My body forgot the urge to smoke." This means that insular cortex activity is related to consciousness of the bodily urge to smoke, and this can be disrupted as a result of insular cortex damage. Based on these results, it can be suggested that the insular cortex, which is associated with the conscious feeling of bodily needs, is an important region of the brain with regards to neural mechanisms of addiction (Naqvi & Bechara, 2009).

Insular Cortex and Self

Based on these neural findings about emotion, feeling, and addiction, it can be assumed that the neural activations of the insular cortex are related to consciousness about self. This assumption is supported by neuroscience studies examining other psychological states, including those focusing on agency. Agency refers to the capacity to proactively change one's circumstances for the better (Bandura, 2001; Deci & Ryan, 1991). The neural basis of agency has generally been examined by comparing the neural activations of self-generated behavior to those of other-generated behavior (Gallagher, 2000; Haggard, 2008). In particular, some agency research has found that the insular cortex showed greater activations for self-generated behavior than for other-generated behavior (Farrer, Franck, Georgieff, Frith, Decety & Jeannerod, 2003; Farrer & Frith, 2002).

Our neuroscience studies have also found that the degree of insular cortex activity was related not only to who initiates and regulates certain behavior but also to whether the underlying reasons for the behavior are from the "pure self" or from social influence (Lee & Reeve, 2013; Lee et al., 2012). That is, the anterior part of the insular cortex showed greater activations when participants imagined their own behavior based on their own intrinsic reasons (e.g., interest and curiosity) than when they imagined their own behavior based on socially emphasized values (e.g., reputation and external rewards). Based on these results, it can be assumed that insular cortex activity is important in the processing of agency and is specifically related to consciousness of the "pure self" (e.g., one's own needs or interests).

CONNECTING NEURAL FINDINGS TO THE PSYCHOLOGICAL THEORIES OF INTRINSIC MOTIVATION

According to neuroscience research on intrinsic motivation, insular cortex activity and striatum activity are core neural bases of intrinsic motivation. These neural findings are in line with the existing psychological understanding of intrinsic motivation. Self-determination theory is one of the most influential theories explaining the nature of human motivation, particularly the nature of intrinsic motivation (Deci & Ryan, 1985; Ryan & Deci, 2000). According to the theory, intrinsic motivation is defined as a type of motivation in which behavior is energized and directed by expression from the self (e.g., interest and curiosity).

The forces that initiate and regulate human behavior in this theory may be related to the neural activations of the striatum, which is known to be related to reward processing and behavior initiation (Cardinal et al., 2002; McClure et al., 2004). This idea has been also suggested by other intrinsic motivation researchers (Braver et al., 2014; Gruber et al., 2014). In contrast, the neural findings from our neuroscience studies additionally suggest an important role of insular cortex activity in the neural system of intrinsic motivation (Lee & Reeve, 2013; Lee et al., 2012). That is, the sources of intrinsic motivation (i.e., the expression from the self) in self-determination theory may be related to the neural activations of the insular cortex, which is well known for its role in conscious feelings about the self (Bechara & Damasio, 2005; Craig, 2009).

Self-determination theory views the major distinction between intrinsic and extrinsic motivation as being based on the degree of self-determination. That is, the degree to which a particular motivation is intrinsic or extrinsic can be predicted by the degree to which the initiation and regulation of behavior is self-determined. This conceptualization influences how self-determination theorists view agency. Deci and Ryan (1991) believe that the involvement of the "pure self" is important in the definition of agency. This means that agency that is fully influenced by the pure self may be qualitatively different from agency in social cognitive theory which is heavily influenced by social context (Bandura, 2001). The theoretical importance of self-determination (i.e., agency) is consistently supported by neural findings related to intrinsic motivation. The degree of agency is closely related to the degree of insular cortex activity, which provides a conscious representation of self-related information (e.g., bodily needs) (Lee & Reeve, 2013).

These findings support the idea that intrinsic motivation is more based on the "pure self" than is extrinsic motivation and that the neural representation of the "pure self" (i.e., insular cortex activity) is important when distinguishing between intrinsic and extrinsic motivation.

CONCLUSION, LIMITATIONS, AND FUTURE DIRECTIONS

Although we are widening the current neuroscientific understanding of intrinsic motivation, there are several remaining issues. According to self-determination theory, human beings have three innate psychological needs (autonomy, competence, and relatedness), and the satisfaction of these three basic needs is important determinants of intrinsic motivation (Deci & Ryan, 1985; Ryan & Deci, 2000). However, few studies have dealt with the fundamental issue of whether the satisfaction of these needs is processed by different neural mechanisms or a single common neural mechanism. Future research is required to clarify this issue. In addition, we need to explore which neural substrates of intrinsic motivation generate the beneficial effects of intrinsic motivation in human learning. Many neuroscience studies have already demonstrated the positive effects of increased striatum activity in memory enhancement or resilience in the face of failure (Gruber et al., 2014; Kang et al., 2009; Murayama et al., 2015). The next step would be testing the effects of increased insular cortex activity on human learning; it is important to test whether different neural substrates of intrinsic motivation (e.g., striatum activity and insular cortex activity) act alone or interact in their influence on human learning.

Despite these remaining issues, the current neuroscientific understanding of intrinsic motivation, which emphasizes the role of both the insular cortex and the striatum, has several implications. Above all, this approach provides neuroscientific evidence supporting the qualitative differences between intrinsic and extrinsic motivation. Of course, it is difficult to disagree with the assumption that there could be a common neural system for the two different types of motivation because they share common psychological properties (e.g., initiation of approaching behavior). But what our program of research additionally shows is that intrinsic motivation and extrinsic motivation are two qualitatively different types of motivation, and that the unique neural base of intrinsic motivation is anterior insular activity. While it is easy to understand rewards as a key component of extrinsic motivation, our program of research suggests that it may be just as easy to understand satisfaction as an important part of intrinsic motivation. Intrinsic motivation is an experience of interest or enjoyment that derives from seeking out novelty and challenges and satisfying curiosity and competence. The message may be that teachers should not underestimate such intrinsic motivational processes in the design and delivery of their instruction, especially since intrinsic enjoyment and satisfaction have been strongly linked to outcomes such as engagement and conceptual learning.

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MOTIVATED COGNITION: NEURAL AND COMPUTATIONAL MECHANISMS OF CURIOSITY, ATTENTION, AND INTRINSIC MOTIVATION

Jacqueline Gottlieb, Manuel Lopes and
Pierre-Yves Oudeyer

ABSTRACT

Based on a synthesis of findings from psychology, neuroscience, and machine learning, we propose a unified theory of curiosity as a form of motivated cognition. Curiosity, we propose, is comprised of a family of mechanisms that range in complexity from simple heuristics based on novelty, salience, or surprise, to drives based on reward and uncertainty reduction and finally, to self-directed metacognitive processes. These mechanisms, we propose, have evolved to allow agents to discover useful regularities in the world – steering them toward niches of maximal learning progress and away from both random and highly familiar tasks. We emphasize that curiosity arises organically in conjunction with cognition and motivation, being generated by cognitive processes and in turn,

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motivating them. We hope that this view will spur the systematic study of curiosity as an integral aspect of cognition and decision making during development and adulthood.

Keywords: Intrinsic motivation; active learning; memory; attention; metacognition; development

INTRODUCTION

Countless studies in neuroscience and psychology have probed the neural basis of cognitive functions such as attention, memory, and mental representations. While these studies have traditionally remained independent from studies of decision making and motivation, this separation is beginning to change with the advent of evidence documenting strong effects of motivation on memory (reviewed in this book). These recent results suggest a more integrative view, whereby cognition and motivation are tightly intertwined. According to this view cognition is not a passive process that is simply "given" to us by the brain, but instead an active, motivated process – a mental act which, much like our physical acts, is proactively oriented toward a goal. Moreover, cognition is a source of motivation, and specific cognitive factors related to learning, memory or attention can causally impact motivational states.

This more integrative conception raises fundamental questions about the types of motivation that drive us to *think*. What are the factors that motivate us to learn, memorize or otherwise process new information? How do these intellectual drives serve our ability to thrive in the world, how do they control our actions and what are their neural substrates?

In this chapter, we will examine these questions with a focus on curiosity – a complex cognitive process that is defined as the intrinsic desire to learn or obtain information. Curiosity reaches its pinnacle in human beings in pursuits such as scientific research, and is arguably a key factor in the considerable success of our species. However, our understanding of curiosity is in its infancy, and its computational and neuroscientific basis are only beginning to be investigated.

We will review recent developments in neuroscience, cognitive psychology, and computational modeling and machine learning that pertain to these questions. We will start by reviewing fundamental properties of curiosity and intrinsic motivation, followed by a survey of recent evidence that curiosity recruits motivational systems (including midbrain dopaminergic neurons and dopamine-recipient structures) and systems of selective attention including parietal areas involved in oculomotor control. Finally, we will review a number of factors that contribute to curiosity, including novelty, surprise, uncertainty, rewards and metacognitive control, and our current understanding of their neural mechanisms.

Throughout the discussion we will stress the idea that curiosity involves a family of mechanisms which, while highly sophisticated in humans, have their roots in more primitive motivational and information sampling systems that are found in many animal species. In addition, we emphasize the fact that mechanisms of curiosity-driven learning can be computationally modeled, and that such models are highly useful in formulating new hypotheses about the nature and function of curiosity in learning, development and behavior.

CURIOSITY AND INTRINSIC MOTIVATION

In Mark Twain's legendary book *Tom Sawyer,* Tom, a lovable and rambunctious teen, says this about intrinsic motivation: "*Work consists of whatever a body is obliged to do, and Play consists of whatever a body is not obliged to do*." In the more formal (though perhaps less entertaining) language of science, an intrinsically motivated activity is one that is undertaken for no apparent reason except the behavior itself (Ryan & Deci, 2000a, 2000b).

Intrinsically motivated behaviors include behaviors that subjects are not obliged to do for survival and yet are highly motivating – such as children's play and adult leisure-time hobbies and creative pursuits. Intrinsically motivated activities are generally pleasurable, and can even cause special states of "flow" characterized by intense feelings of effortless control, concentration, enjoyment, and a contraction of the sense of time (Csikszenthmihalyi, 1990).

From a computational perspective, intrinsically motivated behaviors can be characterized similarly to other goal-directed behaviors– as actions that seek to maximize an internal goal – formalized mathematically as a reward (value) function. A particular challenge however, is to understand what are the value functions that the agents seek to maximize. Whereas, in the vast majority of experiments in neuroscience and psychology, behavior is shaped using easily measurable extrinsic rewards such as money, juice, food, or points, intrinsically motivated behaviors depend on internal factors that are much more difficult to characterize and are related to the individual's affective or cognitive structure. For instance, when creating a painting, an amateur individual may be motivated by the simple pleasure of gazing at the painting, the satisfaction of achieving personal goals (e.g., personal growth, learning, mastering a challenge), the satisfaction of achieving social goals (e.g., impressing her husband) or even the prospect of eventual material gains (being unexpectedly discovered and becoming a successful painter). These constructs can all be viewed as "rewards" in the widely accepted view of the term – as any factor that reinforces behavior and "makes you come back for more" (Thorndike, 1911). However, it remains a formidable challenge to identify which of these internal rewards come into play in any given context and how these motivations are computed by the brain.

Curiosity is a particular system of intrinsic motivation that drives agents to learn. The curious agent seems to have satisfied all his material needs – for food, social contact, safety, etc. As Tom Sawyer would say therefore, the agent has no more *Work* to do and a perfectly rational action that he may choose to take is simply conserve energy and do nothing at all – wait quietly until new primary needs arise. And yet, at least in some circumstances, the agent becomes intrinsically motivated to explore – and he expends time and effort to open a closed door (answer a question), and discover new parts of his environment that were not suspected before. What motivates the agent to carry out this extraordinary behavior? Why incur significant costs in energy, effort, and time, to pursue an uncertain (indeed, unknown!) reward when one's material needs have been satisfied?

A second remarkable aspect of curiosity, beyond its mere existence, is the fact that it generates not a random but a structured pattern of investigation. The agent in our cartoon is not interested indiscriminately in all the information that surrounds him, but becomes curious about specific items. Work in machine learning and robotics clearly shows that, because many of the tasks we may choose to explore in a natural environment are *unlearnable* or impossible to master, agents cannot assign "intrinsic" value to all sources of information as is sometimes claimed in the literature. An indiscriminate strategy of examining all the available information would result in collecting disparate pieces of information with nearly no discovery of useful structures, especially given the limited time and energy available over a biological life span. Therefore, a successful curiosity mechanism must assign value to possible endeavors very selectively, and in a way that maximizes the agent's ability to predict his environment over vast portions of the learning space and on longer time scales. Computational studies show that, in environments that change quickly and/or continuously, curious individuals can gain an advantage by acquiring new skills and discovering new environmental structures (Singh et al., 2010; Barto, 2013). However, this long-term (evolutionary) advantage cannot specify the agent's actions on shorter time scale. Herein lies the second great mystery of curiosity: how do agents achieve structured exploration in a way that maximizes the long-term advantage, given that the specific goals are unknown when the exploration unfolds?

Emerging neuroscientific evidence, to which we turn next, suggests that implementing this system requires the concerted action of dopaminergic systems implicated in value and motivation, and cortical systems mediating cognitive processes of memory and attention.

DOPAMINERGIC SYSTEMS THAT PROCESS PRIMARY REWARDS ARE ACTIVATED BY CURIOSITY

To examine the motivational systems that are recruited by curiosity, Kang et al. used functional magnetic resonance imaging (fMRI) to monitor brain activity in human observers who pondered trivia questions (Kang et al., 2009). After reading a question, the subjects rated their curiosity and confidence regarding the question and, after a brief delay, were given the answer. The key analyses focused on activations during the *anticipatory* period – after the subjects had received the question but before they were given the answer.

Areas that showed activity related to curiosity during this epoch included the left caudate nucleus, bilateral inferior frontal gyrus (IFG), and loci in the putamen and globus pallidus (Fig. 1). In an additional behavioral task, the authors showed that subjects were willing to pay a higher price to obtain the answers to questions that they were more curious about – that is, could compare money and information on a common scale. They concluded that the value of the information, experienced as a feeling of curiosity, is encoded in some of the same structures that evaluate material gains.

Two recent studies extend this result in non-human primates by reporting that midbrain dopaminergic (DA) cells and cells in the orbitofrontal cortex (OFC), a pre-frontal area that receives DA innervation, encode the anticipation of obtaining reliable information from visual cues

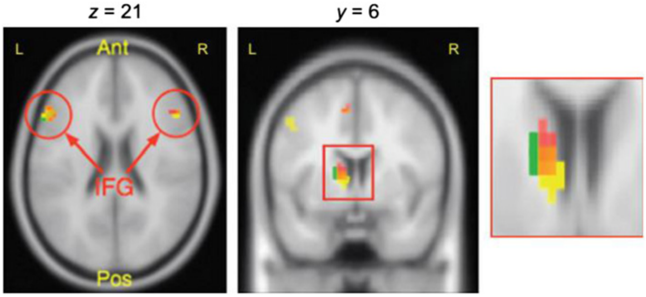

Fig. 1. Brain regions that showed differential activity in high- versus low-curiosity trials during the first question presentation in Kang et al. (2009). Colored areas showed greater anticipatory activation on high-curiosity trials in experiment 1 ($p < .001$ uncorrected, prep > .99, extent threshold 5) using a median-split analysis (red), the modulator analysis (yellow), and the analysis of residual curiosity (green). See the original paper for a color rendition. The illustration at the right is a close-up view of the overlapping caudate activations. Ant, anterior; Pos, posterior; L, left; R , right; IFG, inferior frontal gyrus. *Source*: Reproduced with permission from Kang et al. (2009).

(Blanchard, Hayden, & Bromberg-Martin, 2015; Bromberg-Martin & Hikosaka, 2009).

In the study on DA cells, the subjects were trained on the so-called "observing paradigms," where they had to choose between observing two cues that had equal physical rewards but differed in their offers of information (Bromberg-Martin & Hikosaka, 2009). Monkeys began each trial with a 50% probability of obtaining a large or a small reward and, before receiving the reward, had to choose to observe one of two visual items. If the monkeys chose the informative cue, this cue changed to one of two patterns that reliably predicted whether the trial will yield a large or small reward. If the monkeys chose the uninformative item, this item also changed to produce one of two patterns, but the patterns had only a random relation to the reward size.

The key feature of the behavioral task was that the extrinsic rewards that the monkeys received were equal for the two options (both targets had a 50% probability of delivering a large or small reward), and therefore there was no biological imperative for the monkeys to choose either option. Nevertheless, the monkeys developed a reliable and consistent preference for choosing the informative cue. A subsequent study of area OFC showed that the monkeys will chose the informative option even if its payoff is slightly lower than that of the uninformative option – that is, monkeys are willing to sacrifice juice reward to view predictive cues (Blanchard et al., 2015). Finally, neuronal recordings showed that DA and OFC cells anticipated the receipt of reward information, and encoded the value that the monkeys placed on this information independent of the value of obtaining the reward itself.

Together, these investigations show that, in both humans and monkeys, the motivational systems that signal the value of primary rewards also signal an intrinsic desire to obtain information, raising important (and hotly debated) questions about the computations that relate values based on the two factors.

EYE MOVEMENTS AND ATTENTION

Although DA neurons and DA-recipient structures may enhance arousal and motivation in anticipation of information gains, they are not sufficient to explain the full scope of information seeking mechanisms. In addition to the motivational signals conveyed by these cells, the brain must construct a *full exploration policy* that specifies when, for how long, and from which source to gather information. Constructing such detailed policies requires input from cognitive processes that evaluate the semantic and informational properties of competing cues and their desirability as targets for exploration.

While little is currently known regarding these links, a recent study by Gruber and colleagues (Gruber, Gelman, & Ranganath, 2014) showed that a higher level of curiosity is associated with better memory performance, and enhanced activation of parahippocampal structures and its DA projections, providing valuable first evidence for a link between curiosity and memory. In addition, another recent study in our laboratory revealed a link between curiosity and attention (Baranes, Oudeyer, & Gottlieb, 2015).

In that latter study, we combined eye tracking with a trivia task similar to that used by Kang et al., in which we presented subjects with trivia questions and monitored their eye movements while they were waiting for and reading the answer. As shown in Fig. 2a, questions that were rated as eliciting higher curiosity were associated with faster anticipatory gaze shifts to the expected location of the answer. The subjects' eye position at the beginning of a trial was initially distant from the location where the answer was expected to appear (Fig. 2a, left panel: −1,500 ms), but gaze gradually

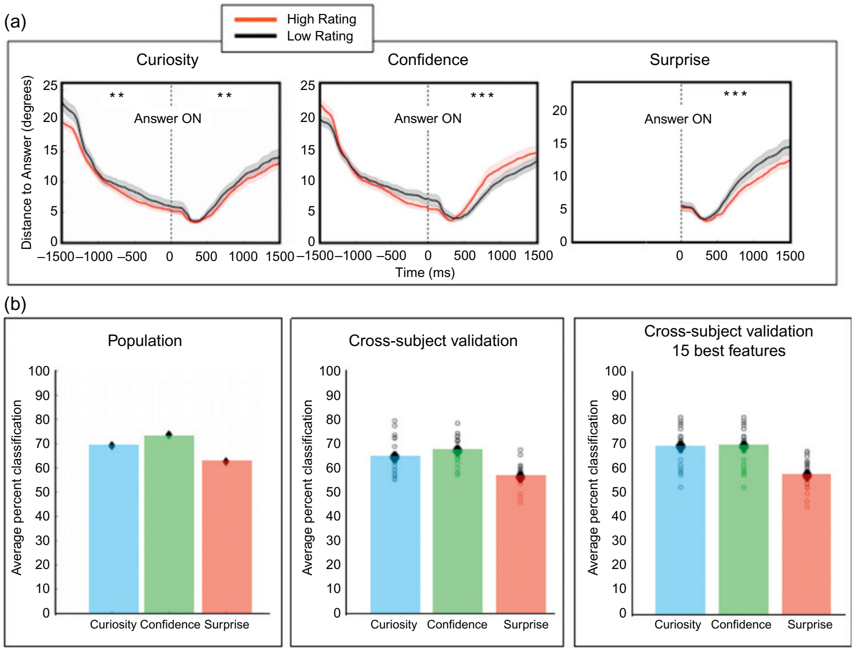

Fig. 2. Curiosity affects eye movements. (a) Eye movement patterns in relation to curiosity, confidence and surprise. For each trial with high or low ratings (black vs gray traces), we computed the distance between the eye position and the left edge of the answer box as a function of time. Distances were averaged for each subject, and we display the mean and SEM across subjects. Average distances before and after answer onset were compared with a one-way ANOVA; $**p < 10^{-45}$, $***p < 10^{-75}$. (b) Classification accuracy for different implementations of a machine learning algorithm. Left: Classification across the entire data set. Middle: Classification with across-subject cross-validation. Right: Same as the middle panel but using only the 15 most informative features. In the middle and right panels, the open points show individual subject predictions and the black points and bars show average and SEM. *Source*: Reproduced with permission from (Baranes et al., 2015).

shifted to the answer location in an anticipatory fashion, well before the answer actually appeared (time 0 in the figure). Anticipatory eye movements were faster for questions that elicited high relative to low curiosity (black vs gray traces, left panel in Fig. 2a) and, across individuals, the magnitude of this acceleration was correlated with measures of curiosity-related personality traits (see also Risko, Anderson, Lanthier, & Kingstone, 2012).

As had also been shown by Kang et al., we found that curiosity had an inverted U-shaped relationship with the subjects' confidence that they knew the answer: subjects were most curious about questions for which they had intermediate confidence. In addition, ratings of curiosity were correlated with ratings of surprise: the more curious the subject were in a question, the more surprised they reported being when viewing the answer. Despite these correlations, the three ratings had dissociable eye movement signatures. While curiosity affected primarily anticipatory gaze, confidence and surprise primarily acted after the answer appeared (times 0−1,500 ms), when subjects lingered longer on an answer if they had reported having less confidence that they knew the answer (Fig. 2a, middle panel), and being more surprised after its presentation (Fig. 2a, right panel).

One intriguing possibility raised by these results is that, if eye movements reflect an individual's mental state, they may also be used to infer that state. To examine this possibility, we used a machine-learning algorithm with a cross-validation decoding technique (i.e., training the algorithm to match ratings with eye movement features in a subset of the data, and testing its predictions in a non-overlapping subset). As shown in Fig. 2b (left) the algorithm correctly predicted the subjects' curiosity, confidence, and surprise based on their eye movements alone with above chance accuracy of approximately 70%. Interestingly, classification accuracy was high even when the algorithm was trained and tested with data from different subjects (Fig. 2b, cross-subject validation) and even when we used a smaller set of eye movement features that were discovered to be most informative (Fig. 2b, 15 best features).

These results suggest that curiosity has powerful effects in recruiting memory and attention. While much remains to be learnt regarding these links, the possibility of using eye movements to read out epistemic states of curiosity, confidence or surprise, has exciting potential practical applications in a number of settings including educational situations.

WHAT MOTIVATES CURIOSITY?

Converging evidence suggests that some of the factors that generate curiosity include surprise, novelty, uncertainty about future rewards, and the probability of rewards for of specific items. We review each factor in turn.

Surprise

It has long been recognized that, far from being unbiased, the way in which we sample information from complex visual scenes depends strongly on our knowledge and expectations (Vo & Wolfe, 2015). In the hands of a professional magician, the manipulation of expectations can lead to spectacular misdirection and consequent surprise (Rieiro, Martinez-Conde, & Macknik, 2013). Predictive coding theories suggest that expectations play a key role in orienting attention by predicting away redundant information and freeing resources for detecting significant items (Friston et al., 2013). This systematic removal of information through active prediction may be critical for allowing us to see – and indeed, survive – as without it we may be overwhelmed by the sheer amount of information that our brains have to process.

Studies by Itti and Baldi have shown that surprise, defined in the domain of visual features, attracts human saccades during free-viewing exploration (Baldi & Itti; Itti & Baldi, 2009). Using a Bayesian algorithm combined with computational models of vision, the authors simulated the observers' beliefs about the expected distribution of pixel values at different visual locations, and defined surprise as the extent to which a visual input differed from these expectations. The authors showed that this quantitative metric could predict human free-viewing patterns with greater fidelity and flexibility relative to simpler intensity or contrast-based predictors. As the authors emphasize, surprise differs from standard measures of information in that it ascribes central importance to the observers' beliefs rather than being defined purely by the entropy (uncertainty) of a stimulus set. This makes it very clear that it is not the mere presence of information that attracts our attention, but the extent to which the information confirms or violates our prior expectations.

Novelty

Novelty, in contrast with surprise, is not context-specific but is defined by the total amount of exposure that observers had to a given observation. Novelty can be modeled mathematically as the dissimilarly between a stimulus and the representation of familiar stimuli encoded in the observer's memory (Barto, Mirolli, & Baldassare, 2013).

In a classical approach to reinforcement-learning (RL), novelty is thought to act as an internal reward that is equivalent to extrinsic rewards.

Consistent with this view, novel stimuli activate midbrain DA structures in humans and other animals (Horvitz, 2000; Laurent, 2008; Wittmann, Bunzeck, Dolan, & Düzel, 2007; Wittmann, Daw, Seymour, & Dolan, 2008), and provide a bonus for organizing reward-based exploration (Barto et al., 2013; Brafman & Tennenholtz, 2003; Kakade & Dayan, 2002; Laurent, 2008; Lopes & Oudeyer, 2012). A recent study in our laboratory complements the findings presented above (Fig. 2) and suggests that novelty also recruits attentional resources (Foley, Jangraw, Peck, & Gottlieb, 2014; Peck, Suzuki, Efem, & Gottlieb, 2009). However, in contrast with a traditional RL view, the attention effects of novelty were independent of those of reward.

To compare the ways in which novelty and reward impacted attention, we trained monkeys on a task in which they received visual cues that could be highly familiar or novel and could bring "good" or "bad" news – that is, signaled whether the trial will end with a reward or a lack of reward (Fig. 3a). After presentation of the cue at a peripheral location, the monkeys maintained fixation for a brief delay and then made a saccade to a *separate* target that could appear either at the same or at the opposite location as the cue. In this task therefore, the cues did not allow the monkeys to choose the trial's outcome. Instead, they only brought information and could automatically bias attention toward or away from their visual field location.

We recorded the activity of visually responsive neurons in the lateral intraparietal area (LIP), a cortical area which, together with the frontal eye field (FEF), is implicated in the selection of targets for attention and gaze (Bisley & Goldberg, 2010; Fig. 3b). LIP neurons have visual receptive fields (RF), selectively encode the locations of attention-worthy items, and are thought to provide top-down signals for orienting attention and rapid eye movements (saccades) (Ibid.).

In our task using reward cues, LIP neurons had sharp visual responses if a reward cue appeared in their RF, suggesting that both positive and negative cues transiently attracted attention (Fig. 3c) (Foley et al., 2014; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009). However at slightly longer delays, the orienting response in LIP changed according to the reward signaled by the cue. The neurons maintained slight excitation for a familiar cue that brought good news (Fam+), but developed sustained *inhibition* for a familiar cue that signaled bad news (a dip below baseline firing rates in the Fam− trace in Fig. 3c). Consistent with these neuronal responses, saccades were facilitated if they were directed toward the location of a positive cue (which was excited in the LIP representation) and impaired if they

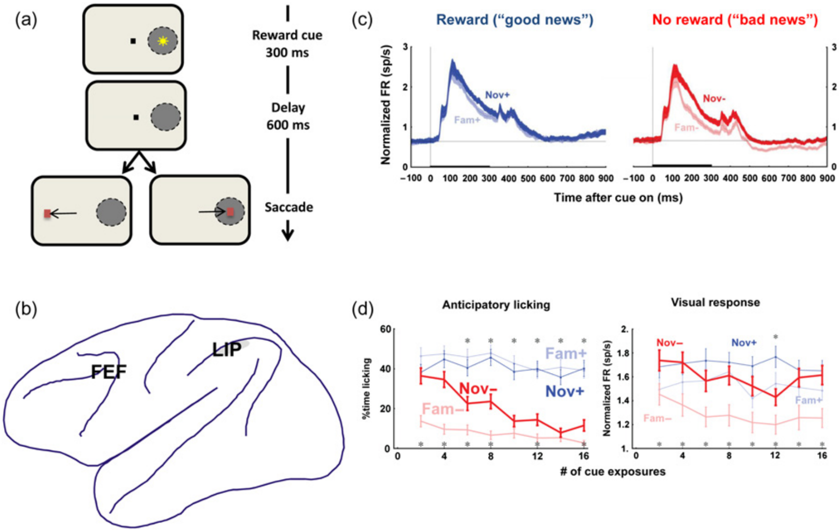

Fig. 3. Independent effects on reward and novelty on visual salience. (a) Task design. A trial began when the monkeys fixated a central fixation point (small black dot). A reward cue was then presented for 300 ms at a randomly selected location that could fall inside the RF of an LIP cell (gray oval) or at the opposite location (for simplicity, only the RF location is illustrated). The cue could fall into one of four categories depending on whether it was familiar (Fam) or novel (Nov) and signaled a positive (+) or a negative (−) outcome. The cue presentation was followed by a 600-ms delay period during which the monkeys had to maintain fixation ("Delay"), and then by the presentation of a saccade target at the same or opposite location relative to the cue. If the monkeys made a correct saccade to the target, they received the outcome predicted by the cue – a reward on Nov+ and Fam+ trials, but no reward on Nov− and Fam− trials. Trials with incorrect saccades were immediately repeated. (b) Cortical oculomotor areas. Lateral view of the macaque brain showing the approximate locations of the FEF and LIP. (c) LIP neurons are modulated by reward and novelty. Normalized activity (mean and standard error (SEM)) in a population of LIP cells, elicited by cues that appeared in the RF and which could be familiar or newly learn and bring "good news" (predicting a reward; Nov+ and Fam +), or bring "bad news" (predicting a lack of reward; Nov− and Fam−). The cues appeared for 300 ms (thick horizontal bar) and were followed by a 600-ms delay period during which the monkeys maintained fixation. The familiar cues showed strong reward modulations, with Fam− cues evoking a lower visual responses and sustained delay period suppression that was not seen for Fam + cues. However, newly learnt cues elicited stronger overall responses and weaker reward modulations. In particular, Nov− cues did not elicit the sustained suppression seen for the Fam− cues. (d) Learning of cue-reward associations as a function of the number of cue exposures during a session. The points show the duration of anticipatory licking and the normalized visual response (during the visual epoch, 150−300 ms after cue onset) as a function of the number of cue exposures during the session. Error bars show SEM. Stars show differences that are significant at $p < 0.01$. Anticipatory licking for the Nov− cues declined rapidly but the visual response elicited by the Nov− cue remained high throughout the session. Although the monkeys rapidly learn negative cue-reward associations, they are slower to reduce the salience of a "bad news" cue. *Source*: Reproduced with permission from Peck et al. (2009) (b) and Foley et al. (2014) (c and d).

were directed toward the location of a negative cue (which was suppressed in LIP). These neural and saccadic effects were spatially specific, occurring at the cue location but not at the opposite visual field location. That is, beyond producing global changes in arousal or motivation, the reward message conveyed by the cues modified the attentional processing of *specific* sources of information.

Comparison of novel and familiar cues showed that these reward-dependent attentional effects were much weaker or absent for newly learnt items, despite the fact that the monkeys quickly learnt the significance of those items. When they were first confronted with a novel cue, the monkeys showed anticipatory licking indicating that they expected to receive a reward following the cue, but this licking quickly extinguished if a cue turned out to signal a negative outcome (Foley et al., 2014) (Fig. 3d, left). However, LIP neurons showed enhanced responses to novel visual cues, and this enhancement persisted for dozens of presentations even for cues that signaled negative or positive outcomes (Fig. 3d, right). That is, newly learnt cues continued to produce enhanced salience and LIP responses on longer time scales, even when the cues signaled "bad news."

As we discussed in the previous section therefore, novelty seems to exert dissociable effects through multiple pathways, both by activating motivational systems and through reward-independent visual/attentional effects. Understanding how these processes work in concert will be an important topic for future investigations.

Reward and Uncertainty

While the factors of novelty and surprise that we discussed above can engage attention independently of the observer's task, attention can also be controlled in a top-down fashion – that is, tightly focused on achieving a goal. Since the early studies of Yarbus in the 1950s it has been appreciated that, when observers are engaged in a task, their eye movements are directed very selectively to task-relevant stimuli with very few glances to salient distractors, revealing the strength and importance of task-related control (Tatler, Hayhoe, Land, & Ballard, 2011).

Some insight into the computational basis of such task-related control comes from studies of naturalistic behaviors where subjects perform tasks such as driving in virtual reality settings (Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Hayhoe & Ballard, 2014; Sullivan, Johnson, Rothkopf, Ballard, & Hayhoe, 2012). Behavior in such contexts was computationally analyzed using RL models that partition the subjects' actions into discrete sub-tasks; for instance, while driving, one may have to coordinate between the sub-task of monitoring the speed and that of monitoring the road. These models suggest that gaze is allocated to competing sub-tasks based on two factors: the rewards and informational demands (uncertainty) of each individual task. This dual control mechanism allows subjects to direct gaze efficiently – to inform those actions that are not only valuable for achieving a goal but also have uncertainty and need for information (Hayhoe & Ballard, 2014; Sullivan et al., 2012; Tatler et al., 2011).

Remarkably, recent findings from our laboratory suggest that dual control by reward and uncertainty may operate even when subjects sample information spontaneously in intrinsically motivated fashion, without being obligated to perform an action (Daddaoua, Lopes, & Gottlieb, 2016). In the paradigm we used in that study, each trial had a different probability of delivering a reward, and monkeys received advance information about the probability that was in effect on a trial (e.g., 0%, 50%, or 100% reward probability; x-axis in Fig. 4). While waiting for reward delivery, the monkeys were given the *opportunity* to obtain additional information by searching for a reward cue that was hidden in a visual display, and which would provide perfect information about whether or not a reward will arrive. Importantly, the monkeys had no requirement to search for the additional cue; the reward arrived according to the signaled probability, whether the monkeys did or did not uncover the cue.

As shown in Fig. 4, the monkeys were intrinsically motivated to search, and their motivation depended on their prior knowledge of the reward probability. Search was almost completely absent if the monkeys expected to obtain no reward (0% likelihood), was maximal if the reward was uncertain (50% probability) and was also quite vigorous if the monkeys had certainty that they would receive a reward (100% likelihood). This pattern remained consistent over the experiment duration (Fig. 4, insets), suggesting that reward and uncertainty shape intrinsically motivated information gathering, similar to their role in instrumental (task-related) settings.

Along with these striking similarities, there are also critical differences between instrumental and non-instrumental settings. In an instrumental context, information guides ongoing actions, and the higher the quality of one's information, the higher the probability of success of those future actions. In contrast, in a non-instrumental context such as the one shown in Fig. 4, subjects cannot improve their chance of obtaining a reward by gathering information. The information the subjects gather can only regulate *their internal state*.

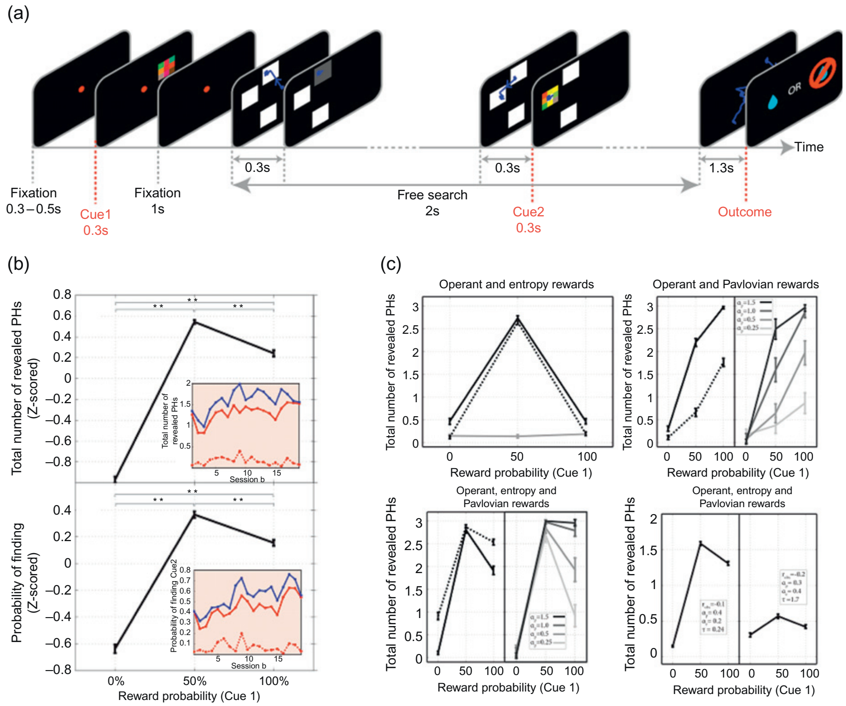

Fig. 4. Intrinsically motivated information search as a function of reward probability. (a) The layout of the task. See text for explanation. (b) The *x*-axis indicates the reward probability that was signaled to the monkey on each trial, before the information search began. The top panel shows the number of items sampled by the monkey as a function at each reward probability (mean and standard errors across all testing sessions (days), after *z*-scoring within individual sessions). The bottom panel shows the probability of finding the hidden cue (mean and standard errors, *z*-scored across all sessions). $*p < 0.025$ (Wilcoxon test). The *insets* in each panel show the average of the raw data in each daily session. The dotted, solid gray and solid black traces indicates 0%, 100%, and 50% reward probability. (c) Model simulations using different value functions. See text for details.

The fact that our subjects were interested in obtaining information when they had reward uncertainty (50% likelihood) suggests that, all things being equal, they prefer to resolve uncertainty as early as possible. The fact that the subjects were also interested in viewing positive cues when they had *no uncertainty* (100% likelihood) is quite remarkable and suggests that the mere act of viewing a positive cue has *intrinsic value*, even if the cue is redundant and cannot be used to guide future actions. This conclusion is consistent with a rich literature showing that animals automatically approach and attend to positively conditioned Pavlovian cues (Castro & Berridge, 2014; Dayan, Niv, Seymour, & Daw, 2006; Flagel et al., 2011; Hickey, Chelazzi, & Theeuwes, 2010a, 2010b; Peck et al., 2009) and suggest that these automatic Pavlovian tendencies are important contributors to intrinsic motivation.

Especially importantly for our purpose, the dual role of reward and uncertainty has a striking resonance with dual-process psychological theories proposing that curiosity arises both from a desire to close "information gaps" (reduce uncertainty, or harvest information), and as a mere feeling of "interest" or "liking" of pleasurable items (Litman, 2007; Lowenstein, 1994). It remains a central question for future research to determine the precise ways in which curiosity is motivated by information gains and conditioned reinforcement from pleasurable cues, and to what extent this dual control may be inherited from more basic behaviors such as the task-related sampling of information.

Learning Progress and Metacognition

The four factors we reviewed above – novelty, surprise, reward and uncertainty – most likely act in combination and explain important aspects of curiosity mechanisms. However, several considerations suggest that, while these factors may be necessary, they are *not sufficient* to explain the full range of curiosity-based exploration.

Novelty and surprise are important heuristics for arousing curiosity, but they have the limitation that they do not necessarily signal significant or learnable environmental properties. A curiosity system that is based only on searching for novelty and surprise would only produce what early researchers called "diversive curiosity" (Lowenstein, 1994) – the type of transient curiosity we may show when we browse the internet with no specific aim – but cannot explain more deliberate, sustained investigative actions such as self-motivated study or scientific research.

Reward and uncertainty, on the other hand, can produce longer-lasting effects, but they are only well defined for highly practiced tasks, and are typically *not known* to agents when they embark on curiosity-driven exploration. For instance, in the tasks we described above the subjects were fully informed about the reward and uncertainty involved in a task (Figs. 3 and 4), but in more realistic settings a curious individual will begin exploring with only vague estimates of these quantities. An agent cannot know the payoffs associated with a curiosity-driven action, and critically important, cannot even know the uncertainty associated with that action or indeed, assume that his investigations will *reduce uncertainty*.

Consistent with these intuitions, formal computational studies confirm that search strategies motivated by novelty, high or low uncertainty, or high or low entropy may be useful in well-delimited contexts, but are inefficient in acquiring knowledge and skills in unbounded large spaces that contain unlearnable tasks (Baranès & Oudeyer, 2009; Lopes & Montesano, 2014; Lopes & Oudeyer, 2010). Computational heuristics that motivate agents to explore states of high uncertainty may cause them to become trapped in random unlearnable tasks; conversely, heuristics that motivate agents to *minimize* uncertainty will cause them to focus exclusively on well-learnt, predictable tasks. To understand the full range of our curiosity, therefore, we must account for the coexistence of two conflicting drives: the desire to reduce uncertainty on a short time scale versus the *intellectual risk taking* and will to increase uncertainty in order to learn on longer time scales.

To address these shortcomings, studies of artificial curiosity have developed computational strategies based on a metacognitive mechanism that assigns value to competing tasks based on the empirical learning progress (LP) related to each task (Baranes & Oudeyer, 2013; Lopes, Lang, Toussaint, & Oudeyer, 2012; Moulin-Frier, Nguyen, & Oudeyer, 2013; Oudeyer, Kaplan, & Hafner, 2007; Schmidhuber, 1991; Srivastava, Steunebrink, & Schmidhuber, 2013). Lopes et al. (2012) proved that exploration based on LP is equivalent to methods based solely on the number of visits (e.g., Brafman & Tennenholtz, 2003) but becomes more robust when encountering changing situations or having the wrong expectations.

LP-driven mechanisms prioritize competing tasks based on the rate of improvement – derivative – of the cost function that the learner is trying to maximize. LP can be defined based on the rate of improvement of predictions of a sensorimotor outcome or of the reward/success rate in a task. Compared to heuristics that search for high uncertainty, LP-driven mechanisms will motivate the learner to investigate situations that are initially uncertain and *keep exploring* them *only if* these situations lead to learning in practice. This can be formulated as an operational implementation of the information-theoretic framework of the free-energy principle (Friston et al., 2015).

An example of algorithmic architecture implementing an LP-driven curiosity process is the R-IAC architecture, detailed in Fig. 5b. In this

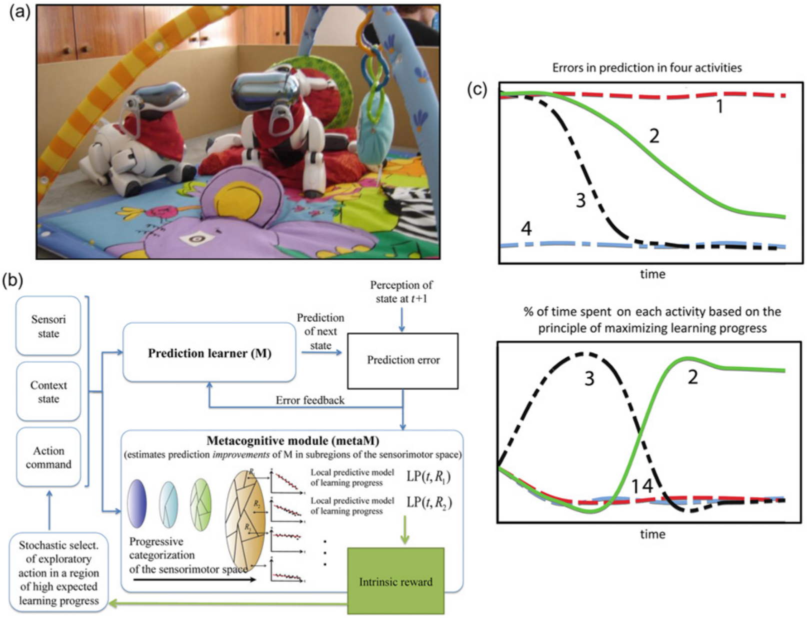

Fig. 5. Spontaneous curiosity-driven exploration can be efficiently driven by searching for situations that improve current predictions (LP), and self-organize a learning curriculum of increasing complexity. (a) The Playground Experiment: a quadruped robot placed on an infant play mat with a set of nearby objects, as well as an "adult" robot peer. The robot is equipped with a repertoire of motor primitives parameterized by several continuous numbers, which can be combined to form a large continuous space of possible actions. The robot learns how to use and tune them to affect various aspects of its surrounding environment, and exploration is driven by maximization of learning progress using the R-IAC architecture. We observe the self-organization of structured developmental trajectories, whereby the robot explores objects and actions in a progressively more complex stage-like manner while acquiring autonomously diverse affordances and skills that can be reused later on. The robot also discovers primitive vocal interaction as a result of the same process. (b) The R-IAC architecture implements this curiosity-driven process with several modules. A prediction machine (M) learns to predict the consequences of actions taken by the robot in given sensory states. A metacognitive module (metaM) estimates the evolution of errors in prediction of M in various subregions of the sensorimotor space, which in turn is used to compute learning progress as an intrinsic reward. Because the sensorimotor flow does not come pre-segmented into activities and tasks, a system that seeks to maximize differences in learnability is also used to progressively categorize the sensorimotor space into regions, which incrementally model the creation and refining of activities/tasks. Then an action selection system chooses activities to explore for which estimated learning progress is high. This choice is stochastic in order to monitor other activities for which learning progress might increase. (c) Confronted with four sensorimotor activities characterized by different learning profiles (i.e., evolution of prediction errors), exploration driven by maximization of learning progress results in avoidance of activities already predictable (curve 4) or too difficult to learn to predict (curve 1) to focus first on the activity with the fastest learning rate (curve 3) and eventually, when the latter starts to reach a plateau, to switch to the second most promising learning situation (curve 2). This allows the creation of an organized exploratory strategy necessary to engage in open-ended development. *Source*: Adapted with permission from (Kaplan & Oudeyer, 2007).

architecture, a robot learns to predict the consequence of its actions. Such predictive learning is made with statistical inference over the data collected when the robot carries out "experiments," that is, tries an action and observes the results. The robot then chooses which task to perform based on a metacognitive module that monitors the evolution of prediction errors in various regions of the sensorimotor space: it selects regions to explore with a probability that is proportional to the rate of improvement in the past (such probabilistic scheme allows to continually search for new niches of progress).

In one study, we showed that such an architecture allows a robot to master hand-eye coordination much faster relative to strategies based on random exploration or a search for maximal uncertainty (Baranès & Oudeyer, 2009). Similar results were shown for the acquisition of other skills such as omnidirectional legged locomotion (Baranes & Oudeyer, 2013) or the manipulation of flexible objects (Nguyen & Oudeyer, 2013)

Interestingly, these analyses showed that, in addition to providing very efficient for acquiring new skills in large task spaces, LP-based algorithms produce exploration strategies that spontaneously progress from simple to more complex tasks in the absence of external instructions. For example, in the Playground Experiment (Fig. 5a) several behavioral and cognitive phases spontaneously formed during learning. After a phase of random body babbling, the robot focused on moving only certain body parts, and then focused on increasingly complex action-object affordances – beginning by learning how its leg can push or grasp objects, and ending up exploring how its vocalizations could produce reactions in another robot. Repeated runs of this experiment showed that in many cases similar developmental milestones appeared in a similar order while other robots showed deviations from these milestones or went through them in a different order, similar to the dual properties of universal tendencies and diversity seen in the development of infants (Oudeyer et al., 2007; Oudeyer & Smith, 2016).

In a related experiment on vocal development, robots used an LP-based algorithm to discover how to communicate with peers (Moulin-Frier et al., 2013). This experiment relied on a physical model of the vocal tract, its motor control and the auditory system, and showed how such a mechanism can explain the adaptive transition from vocal self-exploration with little sensitivity to the speech environment, to a later stage where vocal exploration becomes influenced by vocalizations of peers. Within the initial self-exploration phase, a sequence of vocal production stages self-organized, and shared properties with infant data: the vocal learner first discovered how to control phonation, then vocal variations of unarticulated sounds, and finally articulated proto-syllables. As the vocal learner becomes more proficient at producing complex sounds, the imitating vocalizations of the teacher provide high LP resulting in a shift from self-exploration to vocal imitation.

One can apply such automatic organization of learning in intelligent tutoring systems. These systems' goal is to provide automatic assistance to learners based on their skills. As each student will have their own background, particular strengths, and weakness, a general model equal for all students will not accurately predict the behavior of any particular student. Clement, Roy, Oudeyer, and Lopes (2014) proposed the use of LP measures to allow an intelligent tutoring system to adapt to the particular learning progression of each individual student and showed that different paths provide a faster learning.

A salient property of LP-based curiosity algorithms is that they naturally give rise to a behavioral pattern that is a cornerstone of theories of intrinsic motivation – namely, the tendency of exploratory actions to progress from simpler to more complex tasks (Ryan & Deci, 2000a, 2000b). In a recent study, we replicated the latter effect in a laboratory setting by using a task where subjects were given a set of computer games of variable complexity and could freely choose the games they wished to play (Baranes, Oudeyer, & Gottlieb, 2014). A game lasted several seconds and required subjects to press a key as accurately as possible to intercept a series of dots that streamed past the center of the screen (Fig. 6a). Even though the subjects received no instruction about which game to select, they spontaneously organized their exploration in consistent patterns. Subjects did an initial survey of the entire space of the available games – including the most difficult games where dot speed were very high and performance was low – and then focused their exploration on games of intermediate complexity, where performance was 70–80% correct (Fig. 6b). This general trend was modulated by factors such as how much novelty could be found in games of a given complexity, and how the difficulty of tasks was spread along the game distribution.

Therefore, behavioral evidence is consistent with the idea that a self-organizing pattern based on task complexity shapes intrinsically motivated behaviors in a variety of contexts. However, more evidence is needed to establish whether this pattern indicates an LP-based mechanism. Many forms of learning are nonlinear in time (showing effects such as savings and consolidation) and it is unclear whether subjects can accurately track their LP or which aspects of progress determine intrinsic motivation. Addressing these questions will be critical for a better understanding of our most elaborate curiosity-based forms of exploration.

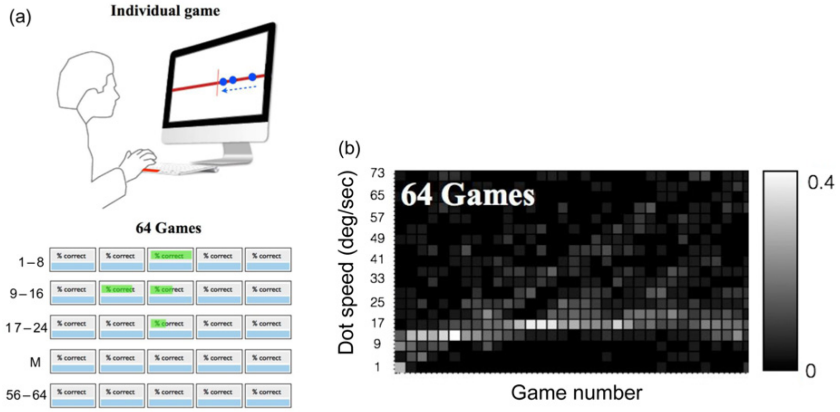

Fig. *6*. Intrinsically motivated exploration in a laboratory game. (a) Task design. The top panel shows an individual game lasting ~30 seconds, in which subjects pressed a key to intercept a stream of moving dots (arrow) as they crossed the screen center. The bottom panel shows the selection screen with 64 games from which subjects could freely choose which game they wished to sample. (b) The speed (difficulty) of the selected games during a session. The color map indicates the probability of selection of a given speed, measured across all subjects in a sliding window over the session. *Source*: Adapted with permission from Baranes et al. (2014).

CONCLUSIONS

We reviewed a theory of curiosity that emerges from a synthesis of findings from neuroscience and machine-learning fields. A central theme that we stressed throughout the review is the fact that curiosity implies a tight interaction between cognitive and motivational systems. Rather than being an external process that acts *on* learning and cognition, curiosity arises organically in conjunction with these processes. When it is engaged in cognitive processing, the brain does more than simply discriminate, encode, and remember information – it also evaluates the epistemic and emotional qualities of these cognitive operations and uses them to generate the "interest" and intrinsic motivation that determine its future engagement with a task.

We have also stressed the fact that the mechanisms that generate curiosity would be ideally adapted to allow agents to discover new and useful regularities in large open-ended spaces that contain unlearnable tasks. This is a formidable challenge for which agents may have no optimal solution, and we proposed that organisms meet this challenge by combining a variety of strategies. These strategies include simple heuristics such as exploration based on novelty, surprise, reward, and uncertainty that may have their roots in simpler active sensing behaviors. In addition, they may include more complex targeted investigations potentially based on metacognitive estimates of LP and information gain. These mechanisms may act in concert to autonomously organize exploration of vast unbounded spaces, steering agents away from overlearnt (low uncertainty) tasks and away from unlearnable (high uncertainty) tasks, toward a middle range where the agent can make LP and discover new structures. While many of the views we outlined remain to be refined and substantiated through future research, we hope that they provide a useful roadmap to the key questions posed by that research.

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PART III
MOTIVATION AND LEARNING

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THE ROLE OF FEEDBACK IN LEARNING AND MOTIVATION

Elizabeth Tricomi and Samantha DePasque

ABSTRACT

Performance feedback about whether responses are correct or incorrect provides valuable information to help guide learning. Although feedback itself has no extrinsic value, it can produce subjective feelings similar to "rewards" and "punishments." Therefore, feedback can play both an informative and a motivational role. Over the past decade, researchers have identified a neural circuit that processes reward value and promotes reinforcement learning, involving target regions of dopaminergic input (e.g., striatum and ventromedial prefrontal cortex). Importantly, this circuit is engaged by performance feedback even in the absence of reward. Recent research suggests that feedback-related brain activity can be modulated by motivational context, such as whether feedback reflects goal achievement, whether learners are oriented toward the informative versus evaluative aspect of feedback, and whether individual learners are motivated to perform well relative to their peers. This body of research suggests that the brain responds flexibly to feedback, based on the learner's goals.

Keywords: Learning; motivation; feedback; striatum; dopamine; reward

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INTRODUCTION

In the classroom and in life, there are many ways to learn new information. However, few are as powerful as learning directly through experience. Making a choice and experiencing the outcome allows an individual to adjust responses that should be improved. Educators, clinicians, and parents often use informative feedback, such as praise for desirable responses and critiques of missteps, to help guide such learning. Feedback is a term

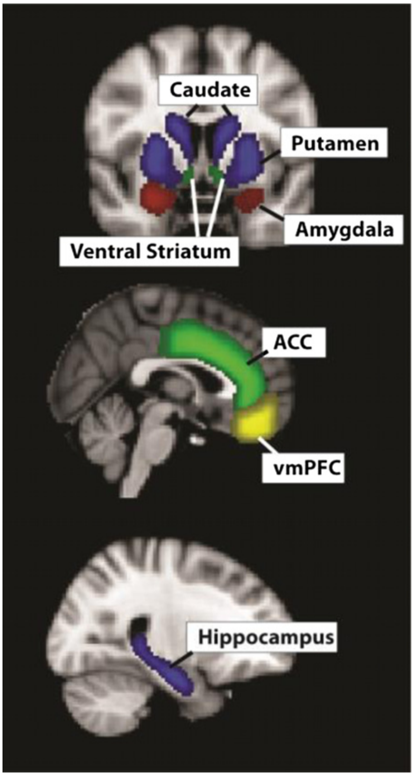

Fig. 1. Components of the Corticostriatal Loops. *Notes*: Dorsal striatum is comprised of the caudate nucleus and putamen, while the ventral striatum primarily refers to the nucleus accumbens. The striatum receives projections from diverse areas, from the anterior cingulate (ACC) and ventromedial prefrontal cortex (vmPFC) to the amygdala and hippocampus.

borrowed from cybernetics; it describes a process by which a response is controlled by its effects (Hill, 1997). In psychological studies of human behavior, the term most often describes stimuli that signal performance accuracy, which can then be used to modify future performance (Kluger & DeNisi, 1996). To motivated learners, feedback not only provides information but also plays an emotive role (Elliott, Sahakian, Michael, Paykel, & Dolan, 1998). The term "positive feedback" indicates an accurate response and can also convey task success, whereas "negative feedback" denotes an inaccurate response and can signify failure or poor task performance.

Most of the time, learners are pleased to receive positive feedback, causing positive feedback to have appetitive value, and thus to serve as a reward (Elliott, Frith, & Dolan, 1997). Since rewards act as reinforcers, which are events that increase the frequency of a behavior (Hill, 1997), positive feedback motivates learners to perform in a way that will maximize their chance of earning more positive feedback. Negative feedback can be viewed either as the omission of the positive hedonic value associated with positive feedback or as an outcome with negative hedonic value (Holroyd & Coles, 2002). In either case, negative feedback typically acts as a punishment, which is an event that decreases the frequency of a response (Miller & Escobar, 2002). Note that punishment should not be confused with negative reinforcement, which refers to the removal of a stimulus of negative hedonic value, which *increases* the tendency to perform a behavior (e.g., a baby's cry, which is eliminated when the baby is picked up; Miller & Escobar, 2002). Negative feedback can thus motivate learners to adapt their behavior in order to minimize the potential for further negative feedback.

Although lab-based learning tasks involving externally provided feedback may seem artificial, they closely mimic ever-present real-life learning situations. In the classroom, many types of feedback can be used to guide learning, including praise/criticism from teachers, marks on exams, grades, etc. Additionally, in many cases, performance of a task itself provides feedback (Goodman, 1998). For example, matching jigsaw puzzle pieces together and shooting a basketball through the hoop provide clear indications of response success, which are simply inherent to the tasks themselves. Learning on the basis of this "task feedback" might be assumed to proceed in a similar way as learning based on external feedback, with the only major difference being whether the source of the feedback is intrinsic to the task or externally generated. This chapter will primarily focus on the effects of external feedback, which is easier to manipulate experimentally and has therefore been studied more extensively.

In this chapter, we will begin with a discussion of the neural circuits underlying feedback processing, with a particular emphasis on the striatum, a key brain region in the reward circuit. We will then discuss the effects of motivation on feedback processing during learning, and we will conclude by discussing the implications of this research for education.

BRAIN CIRCUITS INVOLVED IN PROCESSING REWARD-RELATED INFORMATION

The processing of reward-related information is carried out via corticostriatal "loops," or brain circuits, connecting various subregions of the prefrontal cortex involved in valuation and decision making processes, with the subdivisions of the striatum, which has been implicated in reward, motivation, and action control (Fig. 1). The striatum, the primary input unit of the basal ganglia, receives convergent projections from regions throughout the prefrontal cortex, and sends information back to the prefrontal cortex via the globus pallidus and thalamus (Alexander, DeLong, & Strick, 1986).

The "limbic loop" connects the ventral striatum (i.e., the nucleus accumbens) and ventral caudate and putamen with the ventromedial prefrontal cortex (vmPFC), including the orbitofrontal and medial prefrontal regions (Haber, Kunishio, Mizobuchi, & Lynd-Balta, 1995). In addition to prefrontal input, the nucleus accumbens also receives projections from other limbic regions, such as the amygdala and hippocampus (Haber & McFarland, 1999). This "limbic loop" is involved in motivational and value-related processes (Haber, 2011). The "associative loop" includes the caudate nucleus, located in the dorsal striatum (DS), and the dorsolateral prefrontal cortex (DLPFC), an area that is involved in executive functions, such as working memory, response selection and inhibition, and attentional shifting (Niendam et al., 2012; Packard & Knowlton, 2002). This loop is thought to play a role in cognitive functions, including incentive-based associative learning of whether particular responses lead to positive or negative outcomes (Haber, Kim, Mailly, & Calzavara, 2006).

Importantly, both the prefrontal cortex and the striatum receive modulatory dopaminergic input from the midbrain, and the striatum also projects heavily to the midbrain, forming striatonigrostriatal circuits (Haber, Fudge, & McFarland, 2000). Electrophysiological research in nonhuman primates has demonstrated that dopaminergic neurons in the midbrain play a key role in coding for reward-related information

(Schultz, 1998). These neurons respond with bursts of activity to unpredicted rewards, such as delivery of juice, and show effects of learning; if a reward is consistently preceded by a conditioned stimulus, the neuronal activity occurs at the onset of the predictive stimulus, rather than the reward itself. The absence of a predicted reward, however, causes depression in neuronal firing at the time at which the reward would have occurred (Schultz, Dayan, & Montague, 1997). Thus, the dopaminergic signal can be thought of as coding for both positive and negative "prediction errors," that is, the difference between the reward received and the expected reward (Schultz & Dickinson, 2000), an important signal for learning and shaping of decisions.

Functionally, the striatum has been implicated by both electrophysiological and neuroimaging studies in the processing of primary and secondary rewards (Delgado, 2007). Human neuroimaging studies demonstrate that this region shows activation for expectation and receipt of primary rewards, such as juice (McClure, Berns, & Montague, 2003; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003), and secondary rewards, such as money (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000; Knutson, Westdorp, Kaiser, & Hommer, 2000). Typically, rewards produce a signature response of sustained striatal activation, whereas punishments produce a dip below baseline in striatal signal, before it returns to baseline (Delgado et al., 2000). As the magnitude of a reward, such as monetary value, increases, the striatal reward response also increases (Delgado, Locke, Stenger, & Fiez, 2003). The ventral striatum responds to reward prediction errors (Garrison, Erdeniz, & Done, 2013), and is required for the modulation of action vigor by motivational signals (Cardinal, Parkinson, Hall, & Everitt, 2002). Information from the ventral striatum reaches the DS through ascending striatonigrostriatal loops (Haber et al., 2000), and the DS uses reward-related information to acquire action-outcome associations (Yin, Ostlund, Knowlton, & Balleine, 2005). Together, these data suggest that striatal processing of rewards is important for both learning to predict rewards and learning to act in ways that maximize positive outcomes.

One frontal region that projects to the striatum is the anterior cingulate cortex (ACC), a region that has been widely implicated in a diversity of affective and cognitive functions. The ACC is believed to be the source of the "error-related negativity," a component of the event-related potential that is elicited during error detection, and is therefore thought to play an important role in performance monitoring (Holroyd & Coles, 2002). Given its anatomical connections and functional roles in self-control, performance monitoring and effortful cognition, it has been proposed that the ACC integrates emotional and cognitive information to guide intelligent behavior (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). In addition to its connections with the striatum, the ACC is reciprocally connected with the basolateral amygdala (BLA), which itself has been implicated in value and expectancy processes (Belova, Paton, Morrison, & Salzman, 2007). Inputs from the BLA to the striatum are critical for acquisition of striatal responses to reward-associated cues and reward-seeking behavior (Ambroggi, Ishikawa, Fields, & Nicola, 2008). Finally, the hippocampus plays a key role in learning and memory, and especially in declarative memory (Squire, 2004); interestingly, this region also receives dopaminergic innervation, which may facilitate hippocampus-dependent memory formation (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Lisman & Grace, 2005).

The projections of the vmPFC to the ventral striatum position it to play a critical role in the brain's reward circuitry (Haber et al., 1995). The vmPFC has been implicated in the encoding of reward value and expected reward value of both primary and secondary rewards (O'Doherty, 2004). The medial orbitofrontal cortex (mOFC) is more active following reward than punishment, with activation that is correlated with reward magnitude (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001) and prediction error (O'Doherty, Dayan, et al., 2003). Neurons in the OFC are more sensitive to the specific nature of the reward than dopaminergic neurons; that is, different neurons are tuned to different types of rewards (Schultz, Tremblay, & Hollerman, 1998). With its ability to distinguish the specific nature of different rewards, the OFC may be an important substrate of comparing potential rewards. Both neuroimaging studies and neuropsychology work in patients with vmPFC lesions indicate that this region plays a prominent role in decision making (Bechara, Tranel, & Damasio, 2000; O'Doherty, Critchley, Deichmann, & Dolan, 2003), and animal work suggests a role in the weighing of cost-benefit tradeoffs in reward-based decision making, particularly relating to risk and delay (Walton, Rudebeck, Bannerman, & Rushworth, 2007). Furthermore, the vmPFC may play a particularly important role in guiding behavior based on abstract information, such as social cues (Fellows, 2007; Hampton, Bossaerts, & O'Doherty, 2006; Tricomi, Rangel, Camerer, & O'Doherty, 2010), consistent with evidence suggesting its responses to rewards are modulated by the social context (Ho, Gonzalez, Abelson, & Liberzon, 2012). In light of this evidence, it seems that the contribution of the vmPFC to the "limbic loop" may involve the integration of information about reward value and possible response costs with contextual factors, including motivational states.

Importantly, reward representations in the brain do not depend on absolute values of the rewards, but instead are modulated by contextual influences (De Martino, Kumaran, Seymour, & Dolan, 2006; Nieuwenhuis, Heslenfeld, et al., 2005). For example, the brain is sensitive to "counterfactual comparisons" between the reward obtained and the other possible outcomes, suggesting that rewards and punishments are relative. Brain regions involved in reward processing, including the striatum and the prefrontal cortex, show a "reward" response to earning no money when the alternative is losing money, but show a "punishment" response to earning no money when the alternative is winning money (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; Nieuwenhuis, Heslenfeld, et al., 2005). Similarly, activation in the striatum is influenced by information about the value of unchosen outcomes, and this information influences future choices (Li & Daw, 2011; Lohrenz, McCabe, Camerer, & Montague, 2007). Thus, the brain represents value in a flexible way that takes into account subjective interpretation based on relative preferences.

LEARNING FROM FEEDBACK RECRUITS THE BRAIN'S REWARD SYSTEM

For the affective information provided by rewards and punishments to shape our behavior, we must be able to associate them with the actions that produced them. As a part of the "associative loop," the DS, including the caudate nucleus, plays an important role in learning these associations. A study involving a series of three fMRI experiments found that the head of the caudate nucleus was not significantly activated by monetary rewards and punishments presented randomly in time, nor was it recruited when an anticipatory cue signaled an impending reward or loss. Robust activation in the caudate was found, however, when participants had to respond to a cue by choosing one of two responses and were told that the outcome would depend on whether they chose the correct response; these responses also differentiated between reward and punishment trials. A second condition, for which subjects were told that the required button press did not determine the outcome, produced only weak and nondistinct responses in the caudate (Fig. 2). Therefore, the perception of an action-outcome contingency was found to be the critical factor that governs the recruitment of the caudate nuclei. These results suggest a role for the caudate not as

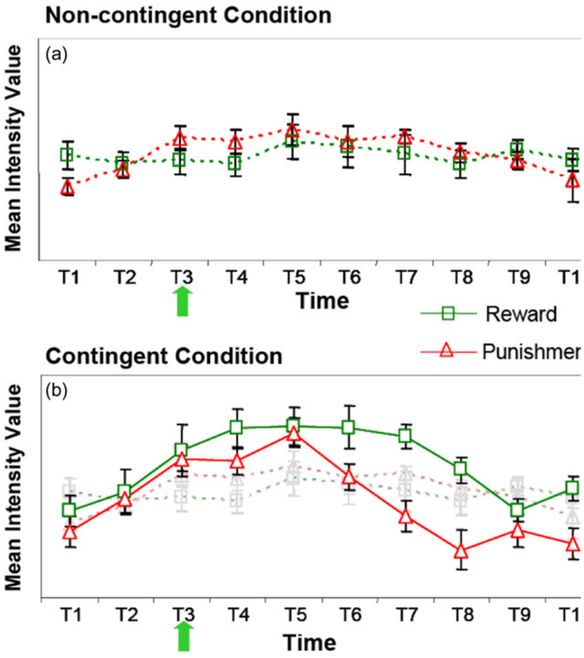

Fig. 2. Rewards and Punishments Elicit Differential Responses Only When Action-Contingent. *Note*: Arrow indicates feedback onset.

a simple reward processor but as a region which associates actions with positive or negative consequences (Tricomi, Delgado, & Fiez, 2004).

Further studies also support the idea that activity in the DS is linked to action. For example, both rewarding and nonrewarding stimuli can activate the caudate if they are behaviorally relevant (Zink, Pagnoni, Martin, Dhamala, & Berns, 2003; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). Additionally, brain regions in the reward circuit, and especially the head of the caudate, have been found to be more active when performing feedback-based learning tasks oneself than when learning based on observing the choices and outcomes for another person (Bellebaum, Jokisch, Gizewski, Forsting, & Daum, 2012; Kobza & Bellebaum, 2015). These action-dependent effects may be particularly apparent in the dorsal, rather than ventral, striatum (O'Doherty et al., 2004), though recent reports have found that the ventral striatum is also sensitive to action contingency and behavioral relevance (FitzGerald, Schwartenbeck, & Dolan, 2014).

The idea that the caudate is involved in adapting behavior based on the consequences of one's actions suggested that it might be sensitive to performance feedback indicating whether one's responses are correct or incorrect during learning, as well as to extrinsic rewards and punishments. To test this hypothesis, one fMRI study investigated whether receipt of performance-dependent feedback in a learning task would activate the caudate in a similar way as extrinsic monetary rewards in a guessing task. The study used as a model system the acquisition of the non-native /r/-/l/ phoneme distinction by native Japanese speakers (Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006), using a phoneme identification training paradigm that had been shown to be effective only when performance feedback was present (McCandliss, Fiez, Protopapas, Conway, & McClelland, 2002). Positive and negative performance feedback produced caudate activation similar to that elicited by monetary rewards and punishments in the guessing task (Fig. 3). Moreover, in contrast to performing the learning task with feedback, phoneme identification practice with no feedback produced neither striatal activation nor successful learning. These results demonstrated that the intrinsic rewards and punishments of positive and negative performance feedback elicit similar neural activity as extrinsic rewards and punishments, and suggested that recruitment of the caudate facilitates feedback-based learning.

Further studies have confirmed that brain regions in the reward system, including the dorsal and ventral striatum, midbrain, and posterior cingulate cortex respond more to positive than negative feedback (Aron et al., 2004; Marco-Pallares, Muller, & Munte, 2007; Nieuwenhuis, Slagter, Alting von Geusau, Heslenfeld, & Holroyd, 2005), and show responses that correlate with reward prediction error (Garrison et al., 2013; Shohamy, 2011). Furthermore, individual differences in feedback-based learning performance correlate with activation in the DS (Schonberg, Daw, Joel, & O'Doherty, 2007) and ventral striatum (Vink, Pas, Bijleveld, Custers, & Gladwin, 2013). The ACC, interestingly, responds more to positive outcomes when they are less frequent than negative outcomes, but more to negative outcomes when they are less frequent than positive outcomes, highlighting this region's role in processing outcomes that are unexpected (Jessup, Busemeyer, & Brown, 2010; Zanolie, Van Leijenhorst, Rombouts, & Crone, 2008). Meanwhile, the prefrontal cortex, including the dorsolateral PFC and inferior frontal gyrus, produces the greatest response to negative feedback when it is the most informative (Tricomi & Fiez, 2008; Zanolie et al., 2008).

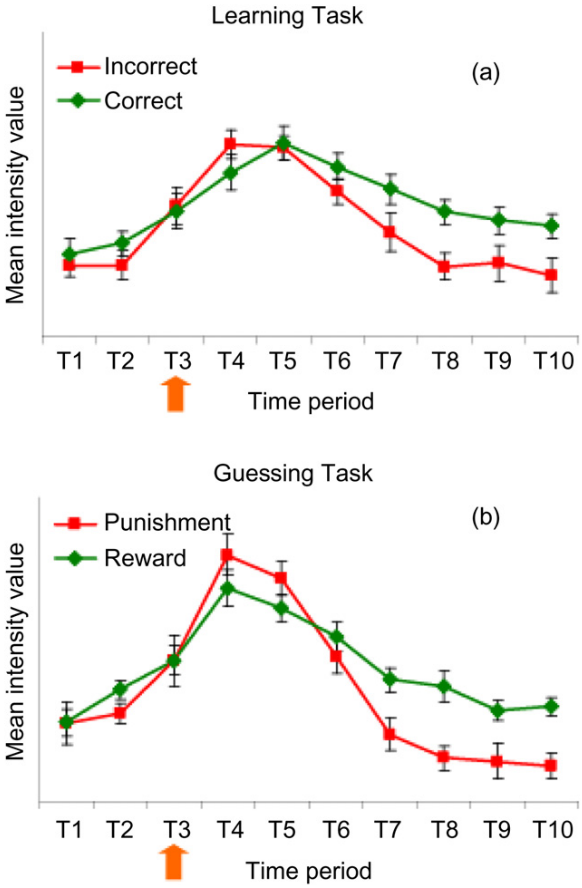

Fig. 3. Positive ("Correct") and Negative ("Incorrect") Feedback Elicit Similar Responses as Monetary Rewards/Punishments.

Along with neuroimaging work highlighting the role of the reward system in feedback processing, neuropsychology studies of patients with Parkinson's Disease, a disease which depletes the brain of dopamine, provide converging evidence for the importance of dopaminergic corticostriatal systems to feedback-based learning. Individuals with Parkinson's Disease are impaired on some learning tasks, but not others. Shohamy and colleagues (2004) found that Parkinson's patients were impaired at feedback-based learning, but were not impaired on a non-feedback version of the same task. This study thus provided critical evidence that feedback processing in particular is dependent on dopaminergic brain systems, and fMRI research confirms striatal dysfunction in Parkinson's patients during the processing of positive feedback (Keitz et al., 2008). Further evidence comes from the work of Frank and colleagues, who investigated how Parkinson's patients learn from positive versus negative feedback (Frank, Seeberger, & O'Reilly, 2004). In healthy participants, learning from negative feedback is more difficult than learning from positive feedback (Hearst, 1991; Kim, Shimojo, & O'Doherty, 2006; Wachter, Lungu, Liu, Willingham, & Ashe, 2009). In contrast, Parkinson's Disease patients learn better from negative feedback than from positive feedback. When these patients are given medication to increase dopamine levels, they become better at learning from positive than from negative feedback (Frank et al., 2004). Frank et al. (2004) suggest that these effects reflect attenuated dopamine neuron firing "bursts" to rewards and augmented "dips" in firing to punishments in Parkinson's patients, a pattern which dopamine medication reverses. Since activity in the striatum and other reward-sensitive brain regions is thought to reflect dopaminergic input, one implication of this theory is that the efficacy of learning from positive and negative feedback should depend on the strength of the "reward" and "punishment" responses they generate in the brain, respectively.

Traditionally, the striatum had been associated with nondeclarative learning, that is, learning without a verbalizable strategy and without an explicit awareness of what is being learned. Yet the use of performance feedback as an instructional tool for the acquisition of declarative knowledge (explicit knowledge of facts and events) is extremely common. If the caudate plays an important role in processing performance-dependent feedback, it would seem unlikely for this role to be limited to nondeclarative learning tasks. Indeed, the deficits shown by Parkinson's patients suggested that the striatum may be particularly important for tasks involving feedback, rather than for all nondeclarative learning tasks (Shohamy et al., 2004; Smith & McDowall, 2006). Further research indicated that the brain's dopamine-mediated reward system facilitated memory formation that was dependent on the hippocampus, a brain structure associated with declarative learning. A feedback-based declarative word pair learning task was developed to test the hypothesis that the striatum would be involved in feedback processing even during declarative memory acquisition. The caudate nucleus does indeed show reward and punishment responses to positive and negative feedback in this task, supporting the notion that this region is critically involved in feedback processing across different types of learning, rather than being solely involved in nondeclarative learning (Tricomi & Fiez, 2008). Furthermore, since the words used on each trial of this task are unique, the experimental design allows caudate activation to be compared for trials associated with high and low confidence on a subsequent post-test. This analysis showed that caudate activation following positive feedback was associated with increased confidence for the same item on the post-test, supporting the role of the caudate in facilitating feedback-based declarative memory acquisition (Tricomi & Fiez, 2012). The results from other studies have also provided converging evidence for the revised view that the striatum and hippocampus are part of interactive, rather than competing, memory systems (Dickerson, Li, & Delgado, 2011; Shohamy & Adcock, 2010; Wittmann et al., 2005).

More recent work on feedback processing has investigated how robust the brain signals to feedback are if they are presented after a delay. Associative learning studies tend to emphasize the close temporal proximity of the response and the corresponding feedback, yet humans are capable of learning from outcomes that are quite delayed from the actions that produced them, such as when a student learns from a graded test that is handed back a week after taking the test. Research with Parkinson's patients found that a delay of only 6 seconds between the response and the feedback was enough to eliminate impairments relative to healthy participants, indicating that dopaminergic brain signals can aid linking actions and outcomes only when they are spaced closely in time (Foerde & Shohamy, 2011). However, an fMRI experiment with healthy participants using the declarative word pair learning task found that if learners are reminded of their original response prior to getting feedback, the same neural structures that respond to immediate positive and negative feedback also respond in a similar way when feedback is delayed by about 25 minutes from the original response. Furthermore, performance was also similar for items learned from immediate and from delayed feedback (Dobryakova & Tricomi, 2013). These findings suggest that the brain structures involved in associative learning are actually quite flexible, and can still be recruited to facilitate learning despite obstacles such as a delay between an action and its consequences.

EFFECTS OF MOTIVATION ON FEEDBACK PROCESSING DURING LEARNING

Recent research on feedback-based learning has investigated how the motivational significance of feedback influences neural processing and consequent learning. Motivation is what drives behavior; thus for feedback to motivate learning, it must be perceived by the learner as aiding in the goal of task mastery. Generally, feedback is treated as having a fixed reward value ("correct"/positive vs. "incorrect"/negative). The subjective value of feedback to an individual, however, can vary depending on how motivated that individual is to earn positive feedback or avoid negative feedback. Correspondingly, feedback signals in the brain have been found to be modulated by the subjective value of the feedback to the individual, not only when feedback is accompanied by monetary reinforcement (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005) but also when no extrinsic reinforcers are present (DePasque & Tricomi, 2015; DePasque Swanson & Tricomi, 2014). For example, a brief motivational interview was used in one study to influence the value learners placed on the goal of doing well on learning task (DePasque & Tricomi, 2015). Based on a technique from motivational interviewing, we used an "importance ruler," in which participants first rated the importance of performing well during the task, on a scale from 0 to 10, and were then asked to explain why they did not indicate a lower number (Miller & Rollnick, 2002). The interview prompted subjects to generate their own personally meaningful reasons to strive for success on the task, with the rationale that self-generated motivational statements would enhance intrinsic motivation for the task more effectively than externally provided reasons (Deci & Ryan, 1987). In a behavioral experiment, those individuals whose motivation increased the most after the interview exhibited the greatest gains in task performance, supporting the notion that within-subject increases in motivation are associated with gains in task performance. In an fMRI adaptation of the experiment, striatal feedback responses were sensitive to individual differences in motivation. Specifically, while many subjects reported increases in boredom or sleepiness during the second half of the scan and evinced decreases in striatal feedback responses after the manipulation, subjects with higher levels of motivation showed attenuation or even reversal of the decrease in striatal feedback responses (Fig. 4).

The idea that responses to feedback in the DS relate to the motivation of the learner is further supported by a study in which the learning goals of participants were manipulated within the context of a single learning task. Han, Huettel, Raposo, Adcock, and Dobbins (2010) used performance-linked monetary rewards to incentivize different types of responses (i.e., "old" vs. "new" judgments) in a declarative memory task. In the absence of monetary incentives, the caudate was generally more active for "old" judgments (identification of words that had been previously studied) than "new," yet when incentivized to make "new judgments," activation in the caudate increased for "new" judgments, even when no feedback was

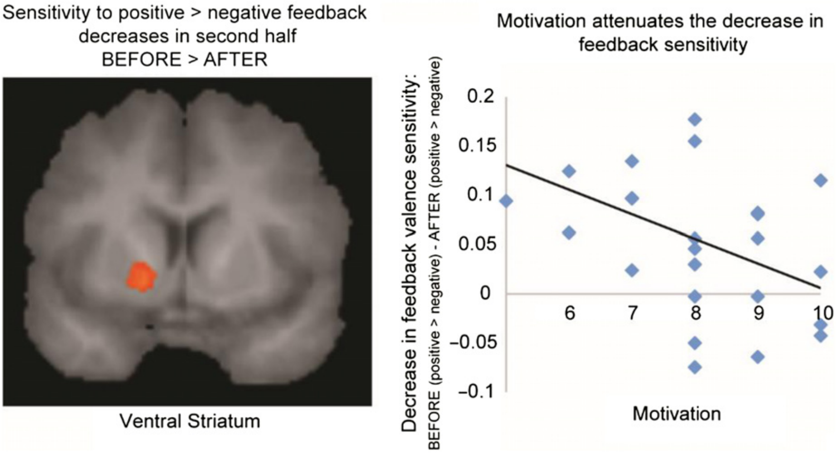

Fig. 4. Motivation Attenuates Decline in Feedback Sensitivity As Task Progresses.

presented. Once again, activation in the caudate appears to relate not specifically to whether a response is correct or incorrect, but rather to whether an outcome satisfies the current goals of the learner.

Another example of how a learner's goals can influence feedback-related brain activation comes from an experiment that compared feedback signals when the feedback provided useful information, but did not indicate performance, versus when it signaled task success. The experiment used a multiple-choice word pair learning task, in which each trial featured a new word pair to learn. Initial feedback provided information about whether the learner had happened to guess correctly, but did not provide evaluative information about task success, since the choices were arbitrary and task success was not under the learner's control. Next, learners were tested again on the same pairs and were instructed to try to pick the correct answer based on their memory from the first set of trials. Feedback during this second phase was thus evaluative, and reflected whether learners were achieving their goal of learning the word pairs. The caudate nucleus was more responsive to positive and negative feedback when it was evaluative than when it was merely informative (Tricomi & Fiez, 2008). Thus, in this example, the DS was engaged by feedback only when the feedback was evaluative of the subject's performance. In contrast, a separate experiment using a similar paradigm with two versus four response options found that varying the amount of information provided by positive and negative feedback could also influence caudate recruitment (Tricomi & Fiez, 2012). With two response options and no initial knowledge of the correct answer, positive and negative feedback provide equal amounts of information: both allow the learner to determine the correct answer. In contrast, with four response options, positive feedback provides more information than negative feedback, since positive feedback indicates that the chosen option is correct, while negative feedback only eliminates one of four possibilities. When responses were arbitrary, positive and negative feedback elicited differential responses in the caudate nuclei with four options, but not with two options. Furthermore, increased caudate activation following positive feedback was associated with better performance for the same item on a post-test. These results suggest that when a learner is oriented to the informational value provided by feedback, even feedback that is not evaluative can engage the caudate and facilitate learning.

Further evidence that feedback signals in the striatum depend on whether feedback is viewed as evaluative versus informative comes from a study which found that simply mixing trials with and without feedback produces different responses in the ventral striatum and head of the caudate to negative feedback and to no feedback, compared to a blocked design of the same experimental task (Lempert & Tricomi, 2015). Whereas positive feedback is typically both rewarding and informative, negative feedback is often punishing, but still informative. When learners did not know whether feedback will be received, however, they reported a preference for negative feedback over no feedback, since even negative feedback provides information necessary to achieve the goal of improving task performance. Correspondingly, the "punishment" signal to negative feedback is attenuated in this "mixed feedback" design, relative to the "blocked feedback" design, within subjects (Lempert & Tricomi, 2015). Because the blocked feedback trials emphasized the evaluative nature of negative feedback (i.e., that negative feedback signals poor performance), they led to the signature "punishment" response of a dip below baseline, relative to no feedback. In contrast, the "mixed feedback" design served to highlight the informative nature of negative feedback, leading to an attenuation of this punishment response (Fig. 5). Thus, even very simple changes in a learning task are capable of shifting the subjective interpretation of feedback and the neural responses it produces.

Much research has shown that reward-related brain signals are strongly influenced by experience-driven expectations, based on the prediction error difference between the value of actual and expected outcomes (Shohamy, 2011). Interestingly, even subjective expectations, such as expectations

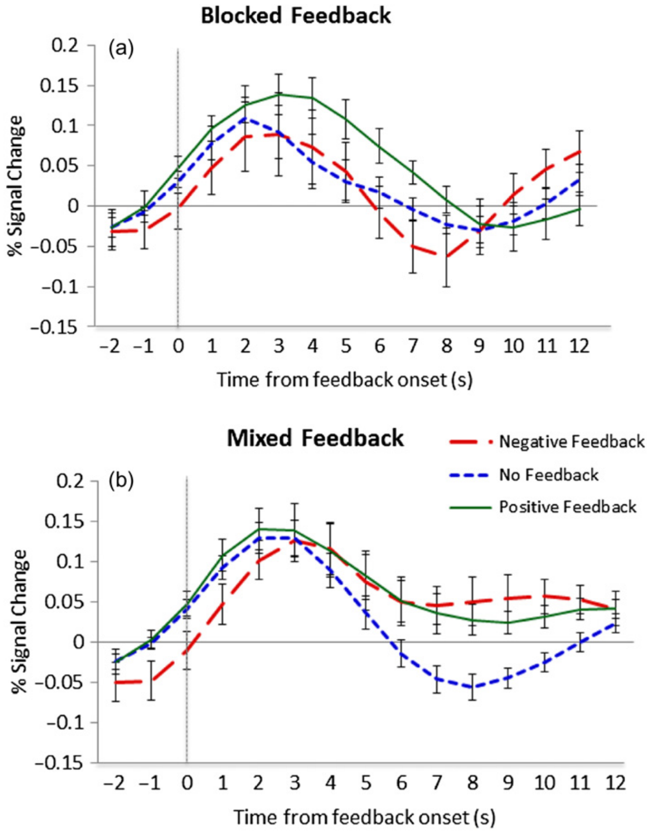

Fig. 5. Mixing Feedback With No-Feedback Reverses "Punishment" Response to Negative Feedback.

based on task instructions, can also influence the neural processing of reward (Delgado, Frank, & Phelps, 2005) and performance-related feedback. For instance, one study employed a trial-and-error categorization task in which separate blocks of trials were labeled either "easy" or "hard." Feedback sensitivity in the caudate was enhanced during blocks that were expected to be more difficult, especially for individuals who scored high in normative goals, which reflect a desire to outperform other students (Fig. 6) (DePasque Swanson & Tricomi, 2014).

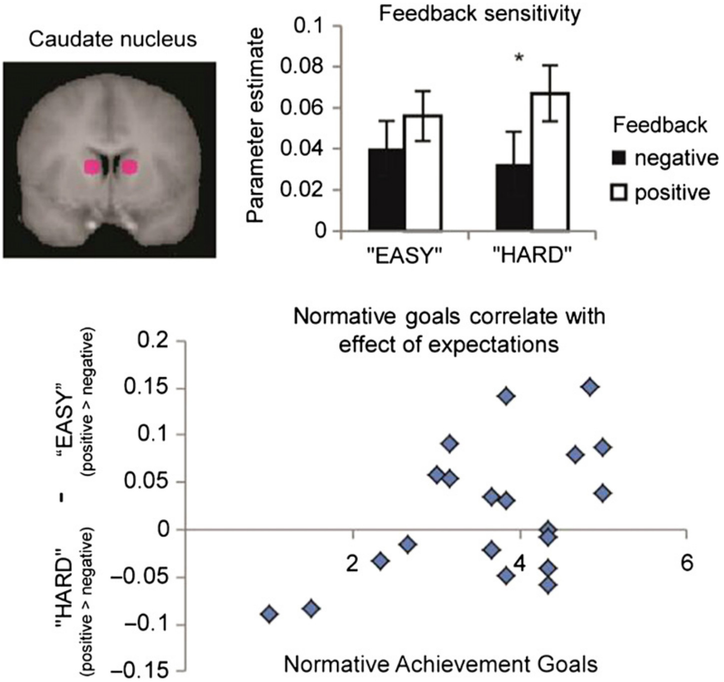

Fig. 6. Expectations of Task Difficulty Modulate Striatal Feedback Responses, Particularly When Normative Goals are High.

Because normative goals are inherently competitive, and difficult tasks could represent a potential opportunity to differentiate oneself from one's competitors, these results imply that individual differences in achievement goals may modulate the subjective value of feedback, thus altering feedback responses in the DS.

These findings highlight the importance of considering individual differences when designing approaches to influence feedback processing during learning. Indeed, individual differences in approach motivation have been linked to exaggerated responses to reward receipt in the ventral striatum and orbitofrontal cortex (Simon et al., 2010), and extrinsic motivation has been found to correlate with neural responses to monetary rewards during probabilistic learning (Linke et al., 2010). Genetic differences in the dopamine transporter (DAT) gene have also been linked to individual differences in the effects of reward on memory, with increased dopaminergic transmission being associated with increased striatal activation to motivational cues and better subsequent memory for those cues (Wittmann, Tan, Lisman, Dolan, & Düzel, 2013).

Together, these findings support the idea that both situational and dispositional factors can influence the subjective value attributed to performance-based feedback, modulating neural responses in networks that play an important role in effective learning and memory. Our research suggests that the effects of beliefs, values, and goals on learning success are tied to the extent to which they influence the incentive value of performance feedback as processed in the corticostriatal reward system of the brain.

THE MOTIVATIONAL CONTROL OF BEHAVIOR AFTER EXTENSIVE EXPERIENCE

Learning is often goal-directed; that is, it is motivated by the desire to achieve a goal, such as receiving positive feedback or mastering a task. However, as learning continues, and a particular response is repeated over and over, behavior may begin to become habitual. Habitual behavior is motivated not by the pursuit of a goal, but rather by a stimulus or context that has become associated with an action that leads to a goal (Dickinson & Balleine, 2002). For example, if someone turns left at a stop sign when driving to work, she may eventually no longer need to represent the goal of getting to work as she drives. Rather, the stop sign serves as a cue that elicits the habitual left turn, which can be executed without thinking about its consequences. This frees up mental resources to think about other things, but can be counterproductive if one's goal changes. Indeed, the hallmark of habitual behavior is that it persists even once the outcome is no longer a behavioral goal. For example, one may still make the habitual left turn at the stop sign, even if one has a doctor's appointment that requires turning right, rather than left.

In the lab, outcome sensitivity can be tested through a selective satiety devaluation procedure, in which individuals are pre-fed one of two food outcomes to satiety, so that the value of that outcome decreases while the value of the other food remains high. If behavior remains goal-directed, response rates should decrease for the devalued outcome relative to the still valued outcome following the devaluation procedure (Balleine & Dickinson, 1998; Colwill & Rescorla, 1985). If, however, behavior has become habitual, the cues associated with each response should elicit similar rates of responding irrespective of the outcome value. This procedure has been used with rats to show that after extensive training, the response to a stimulus becomes independent of the outcome; even if the outcome is devalued, response rates remain high (Dickinson & Balleine, 2002). Further evidence from rodent studies has suggested that distinct subregions of the striatum may contribute to goal-directed and habitual behavior, with the dorsomedial striatum (DMS; equivalent to the caudate in humans) subserving goal-directed action, and the dorsolateral striatum (DLS; equivalent to the putamen in humans) supporting habit-based behavior (Yin & Knowlton, 2006). In rats with lesions to the DLS, habit learning is disrupted (Yin, Knowlton, & Balleine, 2004), whereas DMS lesions interfere with goal-directed learning (Yin et al., 2005); moreover, electrophysiological recordings of neuronal activity have confirmed that DMS neurons are more active early in training, whereas DLS neurons are more active later in training (Yin et al., 2009).

In humans, the selective satiety procedure has also been used successfully to test for outcome sensitivity (Gottfried, O'Doherty, & Dolan, 2003; O'Doherty et al., 2000). As with rodents, human behavior becomes demonstrably outcome-insensitive with extended training, demonstrating the transition from goal-directed to habitual behavior. Furthermore, after extensive training, there is a significant increase in task-related cue sensitivity in the human posterior putamen (Tricomi, Balleine, & O'Doherty, 2009). More recent investigation into the role of the posterior putamen in human habit learning has found that this region encodes reward value at the time a cue is presented requiring a motor response, but not at the time the associated outcome is revealed (Wunderlich, Dayan, & Dolan, 2012). This finding thus fits with the theory that the posterior putamen is not sensitive to outcome value, but rather represents motivationally salient cues. Additionally, Diffusion Tensor Imaging (DTI) has found that individual differences in the strength of the white matter tract between the posterior putamen and the premotor cortex, to which it projects, predict vulnerability to habitual actions toward outcomes that are no longer rewarding. Furthermore, this tendency toward habitual behavior is also related to gray matter density in the posterior putamen, measured with voxel-based morphometry (de Wit et al., 2012). Taken together, these results suggest a rodent-human homology in the neural structures governing goal-directed versus habitual behavior, and show that the distinction between behavior that is motivated by a goal and behavior that is motivated by response-associated cues is related to an underlying distinction in the corticostriatal systems supporting these two types of behavior (Balleine & O'Doherty, 2010; O'Doherty, 2015).

A related line of research has investigated "model-based" learning, in which a learner uses an internal model of the environment to make decisions in a goal-directed way, compared to "model-free" learning, in which action values are learned slowly based on reinforcement history without an explicit model guiding behavior (Daw, Niv, & Dayan, 2005). Although this model-free learning is not insensitive to outcome consequences, it may be one mechanism by which habit learning occurs. Using a widely adopted paradigm with a two-step choice task that can differentiate model-based from model-free learning (Daw et al., 2011), research has found a bias toward model-free learning in individuals with psychiatric disorders related to compulsivity, such as obsessive-compulsive disorder, binge eating, and drug addiction (Deserno et al., 2015; Voon, Baek, et al., 2015; Voon, Derbyshire, et al., 2015); this fits with evidence using other experimental paradigms that habits play an important role in compulsivity, and that stress and anxiety exacerbate habitual tendencies (Alvares, Balleine, & Guastella, 2014; Gillan et al., 2011; Gillan, Robbins, Sahakian, van den Heuvel, & van Wingen, in press). Furthermore, a bias toward model-free learning is associated with lower gray matter volume in brain regions subserving goal-directed behavior, such as the caudate and mOFC, suggesting that compulsivity may arise from an imbalance in contributions from the habit learning and goal-directed learning brain systems (Voon, Derbyshire, et al., 2015). Additionally, a bias toward model-free learning has been associated with increased functional connectivity between the putamen and supplementary motor area, again emphasizing that habit learning is subserved by a corticostriatal loop consisting of the putamen and motor regions of the cortex (Morris et al., 2015).

EDUCATIONAL IMPLICATIONS

An understanding of the multifaceted role that feedback plays in shaping learning has important implications for education and for motivating behavior toward healthy, rather than harmful goals. In trying to understand how to best tailor educational practices to the needs of the individual, influences on learning and performance other than ability need to be considered. Therefore, a better understanding of how motivation influences the neural mechanisms supporting learning and reward processing can inform educational and clinical practices. Our research shows that even in the absence of monetary or other extrinsic incentives, positive and negative feedback can activate learning systems in the brain much like rewards or punishments, particularly in contexts that elicit achievement goals consistent with the objectives of the task. This notion is consistent with studies of intelligence mindsets, in which beliefs about the stability or malleability of intelligence have been shown to influence both affective responses to feedback in the brain and the efficacy with which people learn (Mangels, Butterfield, Lamb, Good, & Dweck, 2006).

Learning can be a goal in itself, and individual differences in achievement goals may endow performance feedback with varying levels of reward value during learning. Interestingly, although performance feedback alone is able to activate the striatum, responses to feedback alone can be undermined by the presentation and subsequent removal of extrinsic monetary rewards. In other words, if an individual becomes accustomed to receiving monetary rewards and those rewards are then removed, striatal activation to feedback alone drops significantly below the response to feedback in a condition where no monetary rewards were ever present (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). This mirrors the behavioral finding on the "undermining effect" of reward on performance; that is, extrinsic rewards such as money can undermine people's intrinsic motivation to perform well on a task for its own sake (Deci, Koestner, & Ryan, 1999). Thus, it is important for educators (and others who wish to promote learning) to adopt an approach to instruction that will not undermine students' intrinsic motivation to learn new material or improve their skills. Subtle changes in the learning context can orient learners toward different achievement goals, which in turn influence the motivational value of feedback. Furthermore, these contextual influences do not act on blank slates; pre-existing differences in individual students' values, beliefs, and achievement goals can alter the way that the learning context affects feedback processing. Therefore, insights into the way that personality as well as contextual variables influence the brain's response to feedback can go a long way in informing educators about how to tailor their practices to best support learning in students who come to the classroom with diverse goals and values.

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MOTIVATIONAL INFLUENCES ON MEMORY

Vishnu P. Murty and Kathryn C. Dickerson[☆]

ABSTRACT

Motivation significantly influences learning and memory. While a long history of research has focused on simple forms of associative learning, such as Pavlovian conditioning, recent research is beginning to characterize how motivation influences episodic memory. In this chapter we synthesize findings across behavioral, cognitive, and educational neuroscience to characterize motivation's influence on memory. We provide evidence that neural systems underlying motivation, namely the mesolimbic dopamine system, interact with and facilitate activity within systems underlying episodic memory, centered on the medial temporal lobes. We focus on two mechanisms of episodic memory enhancement: encoding and consolidation. Together, the reviewed research supports an adaptive model of memory in which an individual's motivational state (i.e., learning under states of reward or punishment) shapes the nature of memory representations in service of future goals. The impact of motivation on

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learning and memory, therefore, has very clear implications for and applications to educational settings.

Keywords: Medial temporal lobe; hippocampus; ventral tegmental area; amygdala; reward; punishment

Motivation is central to human behavior: it affects the decisions we make, the experiences we seek, and consequently what we encode and remember. We often experience ease in remembering something we are motivated to do (e.g., fill out the adoption paperwork for a new puppy), but difficulty in remembering something we are unmotivated to do (e.g., fill out tedious forms at work). Although an extensive literature from behaviorists and learning theorists has studied how learning and memory can be influenced via reinforcement and feedback (Bouton, 2007), relatively little research has focused on how motivational drive influences memory. Similarly, a long history of educational psychology has investigated how feedback and performance testing influence learning (Darling-Hammond, 1994; Kluger & DeNisi, 1996), with comparatively less research investigating how leveraging students' motivational states can facilitate better learning. An emerging literature based on behavioral and cognitive neuroscience, however, has begun to explore the determinants of memory success as they relate to motivation, which has broad implications for and applications to educational settings.

In this chapter, we describe the neural circuitry involved in motivated memory and provide empirical evidence characterizing how motivation directly influences both what and how we remember. We particularly focus on how motivation influences declarative and episodic memory systems. These systems not only support our memory for events but also influence how we retrieve memories to support a variety of adaptive behaviors including reasoning, conceptual knowledge, creativity, decision-making, and future-oriented thinking (Shohamy & Turk-Browne, 2013). To better understand these systems, we integrate converging evidence across animal models and human research that supports a role for motivation in influencing multiple stages of memory, including encoding and consolidation. Furthermore, we delineate how different types of motivational states (e.g., anticipated reward vs. punishment) recruit distinct neural networks to shape what we learn and remember. Lastly, we discuss the implications of these findings for education.

NEUROANATOMICAL SUBSTRATES OF MOTIVATED MEMORY

A substantial body of evidence converging from animal models and human literature implicates the medial temporal lobe (MTL) in memory processes. The MTL consists of the hippocampus and the surrounding parahippocampal gyrus, including perirhinal cortex, parahippocampal cortex, entorhinal cortex, and subiculum. Some of the earliest evidence supporting the role of the MTL in memory came from human patients with damage to the MTL who exhibited profound loss of episodic memories – both an inability to recall past events (retrograde amnesia) and an inability to form new memories (anterograde amnesia) (Squire, 1992). Subsequent animal studies which lesioned or temporarily inactivated parts of the MTL corroborated human patient evidence that the MTL is necessary for episodic memory encoding (Eichenbaum, Yonelinas, & Ranganath, 2007). Furthermore, functional magnetic neuroimaging (fMRI) studies investigating human memory support a role for the MTL in both episodic encoding and retrieval (Kim, 2011; Spaniol et al., 2009).

While the entirety of the MTL is known to support declarative memory, important distinctions have been made regarding the specific functions of the hippocampus proper versus the surrounding MTL cortex (Davachi, 2006; Ranganath, 2010). Namely, these discrete regions within the MTL are thought to support different types of memories. Cortical MTL, which includes perirhinal and parahippocampal cortices, supports the encoding of isolated representations of items and contexts, respectively. In contrast, the hippocampus proper supports flexible, integrative relationships between these unitized constructs and binds them into flexible, mnemonic representations. For example, whereas memory for the cover of your favorite book may only rely on your cortical MTL, memory for the exact location in which you first saw that specific book cover would be supported by the hippocampus.

The MTL does not act in isolation to support human behavior. It is richly connected with a host of brain regions, including areas closely associated with motivation, such as ventral tegmental area (VTA), ventral striatum, and ventral prefrontal cortex (vmPFC), comprising what are known as the mesolimbic (VTA to ventral striatum) and mesocortical (VTA to vmPFC) circuits, which for simplicity we refer to in this chapter collectively as the mesolimbic pathway (Fig. 1). Critically, the interactions of the hippocampus with regions throughout the mesolimbic circuit are thought to support motivation's influence on memory. There are two predominant animal models illustrating how interactions within the mesolimbic circuit facilitate memory. Lisman and Grace (2005) proposed the VTA-hippocampal loop, which describes how newly detected information in the hippocampus is sent as a novelty signal via the subiculum, nucleus accumbens, and

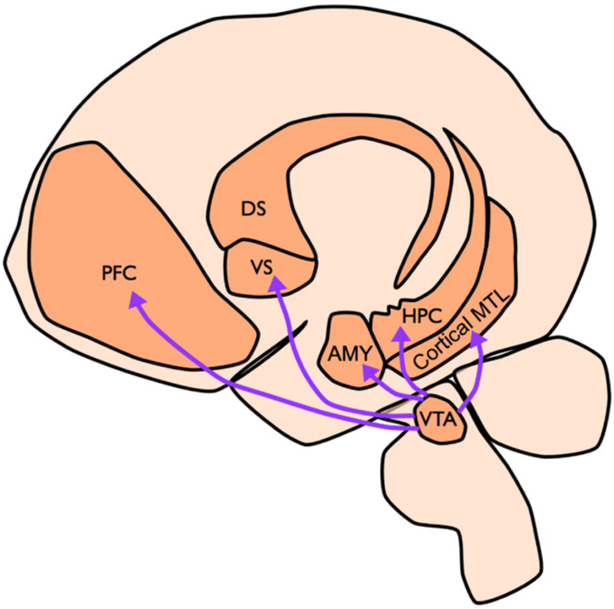


Fig. 1. Key Anatomical Regions Engaged during Motivated Memory Encoding and Consolidation. *Notes*: The ventral tegmental area (VTA) projects dopamine throughout the mesolimbic circuit (depicted here). The hippocampus (HPC) is critical for long-term memory formation and creating rich memories (binding items in a specific context). The HPC and VTA are engaged during reward-motivated memory formation. The amygdala (AMY) and cortical medial temporal lobe (MTL) are engaged during punishment motivated memory encoding (e.g., shocks as opposed to rewards). The prefrontal cortex (PFC) increases signal to noise and may distribute reward information throughout this network. The ventral striatum (VS) encodes reward valuation. The dorsal striatum (DS) is included as a reference point. Anatomical connections are adapted from Shohamy and Adcock (2010).

ventral pallidum to the VTA. Subsequently, neurons in the VTA release dopamine (as a result of novelty signals) into terminals in the hippocampus, facilitating long-term potentiation (LTP). This model therefore emphasizes the loop between the VTA and hippocampus as critical for (1) detection of novel information and (2) encoding novel information into long-term memory.

An alternative model, the hippocampal/neocortical interactions theory of memory formation proposed by Wang and Morris (2010), emphases interactions between the hippocampus and neocortex, rather than the VTA and hippocampus, as critical for memory formation. This model consists of four main components: encoding and storage, cellular consolidation, systems consolidation, and retrieval and reconsolidation. They propose that encoding occurs in the hippocampus formation (HF) and consists of enhancement of activity within cellular (neural) synapses. Cellular consolidation of memories in the HF decay rapidly, but can be augmented if encoding co-occurs with the synthesis, distribution, and capture of new proteins at synapses, which helps to stabilize synaptic changes. Systems consolidation then occurs, wherein the HF establishes memory traces with relevant regions of the cortex. Lastly, during retrieval and reconsolidation, memory traces within the HF are activated and act as a memory index, pointing to regions of the cortex where the memory is fully stored.

The mesolimbic circuit is anatomically connected via dopamine efferent projections originating in the VTA. Dopamine is a neuromodulator with several receptor types (D1–D5), which are largely classified into D1-like (D1, D5) and D2-like (D2, D3, D4). D1-like and D2-like receptors have opposing effects: broadly, they act to increase and decrease, respectively, the responsiveness of neurons they modulate (Pierce & Kumaresan, 2006). Dopamine neurons project from the VTA to receptors in regions throughout the mesolimbic circuit, including the MTL, striatum, amygdala, and prefrontal cortex (PFC) (reviewed by Shohamy & Adcock, 2010). Dopamine is critical for memory formation, as supported by evidence from both the animal and human literature. In the hippocampus, dopamine is a necessary precursor for both LTP – the well-studied cellular model of learning and memory – and the maintenance of long-term memories (Lisman, Grace, & Duzel, 2011; Wang & Morris, 2010). In humans, the effect of dopamine on memory has in part been assessed via pharmacological interventions that act on the dopamine system, including d-amphetamine, methylphenidate, L-dopa, and tolcapone (a COMT inhibitor). On the whole, these studies have shown that dopaminergic agonists improve delayed recall and recognition (or have produced null effects) (Apud et al., 2006; Eckart, Fuentemilla, Bauch, & Bunzeck, 2014; Linssen, Vuurman, Sambeth, & Riedel, 2011; Murphy, Henry, & Weingartner, 1972; Rammsayer, Rodewald, & Groh, 2000). Taken together, converging evidence across animal models and human studies suggest that dopamine facilitates episodic memory.

More recently, human imaging studies using diffusion tensor imaging (DTI) and fMRI have examined the dopaminergic mesolimbic circuit in humans. Evidence suggests the VTA and neighboring substantia nigra (SN) can be delineated in humans using both DTI (Chowdhury, Lambert, Dolan, & Düzel, 2013; Kwon & Jang, 2014) and resting state functional connectivity (Murty et al., 2014; Tomasi & Volkow, 2014). Furthermore, intrinsic connectivity between human hippocampus, VTA, and ventral striatum has been observed during rest (Kahn & Shohamy, 2013), and, critically, intrinsic connectivity between the hippocampus, vmPFC, and large-scale networks has predicted individual differences in flexible learning in healthy, young adults (Gerraty, Davidow, Wimmer, Kahn, & Shohamy, 2014). In the next section, we will explore how motivation directly impacts this mesolimbic circuit to facilitate memory formation.

MOTIVATION INFLUENCES MEMORY ENCODING

In the past decade, scientists have been increasingly interested in understanding the effects of different types of motivational incentives on memory encoding. The majority of studies have examined the effect of monetary reward motivation on memory encoding. However, there are many other types of nonmonetary motivational incentives, including natural reinforcers (e.g., juice), emotional stimuli (e.g., smiling faces), and leveraging people's innate curiosity to learn something new. Furthermore, outside of reward motivation, there are other means of motivating individuals, including punishment. Lastly, in addition to the type of motivational incentive – reward or punishment – other factors significantly contribute to the effects of motivational incentives on encoding including (1) the physiological response elicited by the incentive and (2) the neurobiological substrates engaged during encoding. In the sections below, we describe the effects of each of these motivational incentives in detail, including their influence on both behavior and the neural substrates engaged during encoding.

Effects of Monetary Reward Motivation on Memory Performance

There is increasing evidence in the literature that monetary reward boosts memory for reward-incentivized stimuli (for review, see Miendlarzewska, Bavelier, & Schwartz, 2016). Some studies have incentivized each item to be remembered (e.g., $2 for remembering an upcoming scene), others have directly associated the items with reward (e.g., all animate objects are rewarded) and finally, some have placed items in a rewarding context (e.g., items shown within a high or low reward state). In an exemplar study, Adcock, Thangavel, Whitfield-Gabrieli, Knutson, and Gabrieli (2006) incentivized items to be remembered with either a high ($5) or low ($0.10) monetary reward, and paid participants their full earnings based on memory accuracy on a recognition test the following day. Similarly, Wolosin, Zeithamova, and Preston (2012) incentivized pairs of items with either high ($2) or low ($0.10) monetary reward and paid participants a percentage of their earnings based on memory accuracy. As expected, in both studies, memory was enhanced for high-rewarded compared with low-rewarded memoranda.

In addition to these results, similar findings have been observed when stimuli are incidentally learned (i.e., participants are unaware that they will take a memory test later), rather than intentionally learned (participants are explicitly told their memory will be tested). For example, Wittman and colleagues (2005) adapted a speeded button press task, such that each cue picture belonged to a category (animate or inanimate). The category predicted the possibility of receiving a reward, contingent on participants' successful button press within the allotted time. Participants therefore both anticipated the opportunity to earn a reward and received feedback indicating whether their response was correct or incorrect (rewarded or unrewarded). Memory in a surprise, subsequent memory test was enhanced for reward-predictive compared with non-reward-predictive items. In a subsequent study in which the stimuli were emotional images (positive, negative, or neutral), incidental memory was better for positive-rewarded images compared with the positive-unrewarded images, with no effect of reward on negative or neutral images (Wittmann, Schiltz, Boehler, & Düzel, 2008).

Mather and Schoeke (2011) observed that in studies manipulating both reward anticipation and reward outcome (Wittmann et al., 2005, 2008), the boost in memory due to reward could be caused by the effects of reward anticipation, reward outcome, or both anticipation and outcome. To clarify these findings, Mather and Schoeke (2011) embedded novel stimuli within a cued reaction time task. Participants first saw a cue that predicted the potential to earn a monetary reward ($0.25), avoid a monetary loss (−$0.25), or obtain no outcome (+ $0). They were instructed to press a button as soon as possible when a novel stimulus appeared in order to earn money, avoid monetary loss, or achieve neither monetary gain or loss (control trials). During a surprise memory test, the authors observed that memory was better for items associated with positive outcomes (both gaining $0.25 and avoiding losing $0.25) compared with negative outcomes, regardless of whether or not the positive outcome resulted in an actual monetary gain. These results suggest that in paradigms where there are both reward anticipation and behavior-contingent outcomes, the observed boost in memory may be due to positive outcomes rather than reward anticipation or reward receipt.

Lastly, the effect of embedding items within a rewarding context has been examined. In one such study, Murty and Adcock (2014) embedded novel items in a stream of repeated items under states of high ($2.00) and low reward ($0.10). In a surprise memory test, memory of the novel items was better in the high reward condition compared to both the low reward condition and compared to chance performance, whereas memory in the low reward condition was no better than chance.

In sum, monetary reward boosts encoding of declarative memory via effects of reward anticipation (Adcock et al., 2006; Wolosin et al., 2012), receipt of positive outcomes (Mather & Schoeke, 2011; Wittmann et al., 2005, 2008), and presentation in a rewarded context (Murty & Adcock, 2014). In the next section, we examine the effects of monetary reward motivation on the underlying neural circuitry that may drive these observed behavioral enhancements.

Effects of Monetary Reward Motivation on Neural Systems Underlying Memory Encoding

Results from neuroimaging studies consistently demonstrate activation of the dopaminergic midbrain: in particular, the VTA and hippocampus have been observed during monetary reward-motivated memory (for review, see Miendlarzewska et al., 2016). Interestingly, not only does the magnitude of activation within these individual regions predict reward enhancements on memory, but, critically, the strength of the correlation between VTA and hippocampus activation predicts the memory benefit due to reward (Adcock et al., 2006). These findings suggest that the interactions between the VTA and hippocampus described in animal models are preserved in humans and support reward-motivated memory.

In addition to subcortical areas, regions of the PFC have been shown to interact with the VTA and hippocampus to promote reward-related memory formation (Cohen, Rissman, Suthana, Castel, & Knowlton, 2014; Murty & Adcock, 2014). The ventrolateral PFC has been shown to be engaged during encoding of high-value words and correlated with memory selectivity for high-valued words (Cohen et al., 2014). Further, correlated activity between the VTA and PFC regions predict reward-related hippocampal signals (Murty & Adcock, 2014). Relatedly, it has been observed that reward information is communicated to subcortical areas (including the VTA and ventral striatum) via the PFC (Ballard et al., 2011), which could act as an executive signal to initiate processes enhancing memory for rewarding events.

Notably, the regions described above are within the mesolimbic network. It is hypothesized that the rewarded memory benefit is due to reward-induced increases in dopamine within the network, which facilitates LTP of memoranda. However, evidence to support this hypothesis is tangential at present and includes primarily genetic indices of individual differences in dopamine. In one study, participants were given L-dopa (the precursor to dopamine) while performing a motivated memory paradigm (Sumner, Duffy, Chen, & Adcock, 2013). The authors observed that individuals with low baseline memory performance, as well as genetic profile scores and personality/symptom questionnaires associated with low dopaminergic tone, benefited the most from L-dopa – specifically, the drug increased memory for high-rewarded scenes in these individuals. However, no memory boost was observed with L-dopa in individuals with high baseline memory performance. Similarly, administration of L-dopa has been associated with better episodic memory performance during incidental encoding (Eckart et al., 2014). These studies emphasize that the impact of dopamine on memory performance varies across individuals depending on a variety of factors including genetics and personality traits. Furthermore, these experiments lay the foundation for future work, including direct measurements of dopamine using PET imaging, to confirm the role of dopamine in motivated memory formation.

Effects of Nonmonetary Reward Motivation on Memory Encoding

While a considerable amount of research has focused on the effects of monetary reward motivation on memory performance, there are other methods of motivating individuals, including using natural reinforcers (e.g., juice), emotional stimuli (e.g., smiling faces), and leveraging people's intrinsic curiosity in learning something new. Recent work, adapted from the paradigm developed by Adcock et al. (2006) demonstrated that natural rewards (e.g., juice) also boost memory performance. In this study, instead of receiving monetary rewards based on memory accuracy, participants were promised a liquid reward for memory performance (e.g., water, soda, juice). Memory was better for images paired with a liquid reward compared with no liquid reward (Rainey, Dickerson, & Adcock, 2014).

In addition to natural rewards, social cues can also be interpreted as rewarding stimuli. One study examined the effect of facial expression (smiling faces vs. neutral faces) on memory performance for names paired with each face. The authors observed better memory for names paired with smiling faces than neutral faces (Tsukiura & Cabeza, 2008). Activation of the PFC and hippocampus was greater for smiling than for neutral faces during successful encoding and retrieval of face-name pairs. Furthermore, activation across these regions was more strongly correlated for smiling than neutral faces during successful encoding and retrieval. These findings suggest that engagement of reward motivation via a variety of incentives may facilitate episodic memory.

Lastly, recent work has leveraged people's natural curiosity in learning new information to explore how curiosity impacts memory. In a seminal study by Gruber, Gelman, and Ranganath (2014), the authors showed participants a list of trivia questions and asked them to rank each question according to how likely there were to know the answer and how curious they were to know the answer. For each participant, the experimenters subsequently divided the questions into those associated with high curiosity and low curiosity. Participants were then shown each question inside the MRI machine and, while they were waiting for the answer, they were presented with incidental information (a trial-unique, novel face). Participants' memory was better for both the trivia questions and for the faces associated with high curiosity than low curiosity. The authors observed that activation in the midbrain and ventral striatum tracked curiosity, while the hippocampus displayed greater activation for remembered than forgotten trivia questions only during states of high curiosity. These findings suggest that the same neural architecture supporting monetary reward-motivated states is utilized during states of intrinsic motivation, such as natural curiosity.

Limitations on the Benefits of Motivation on Memory Encoding

The above literatures demonstrate that motivation, induced by a variety of incentives, can facilitate hippocampal function and memory encoding.

Motivation, however, does not always result in better memory performance. Rather motivation can either impair or enhance learning depending on the nature of a performance incentive and how an individual perceives it. Outside of the domain of memory, a large literature has documented how incentivizing performance on a task can lead to worse performance in certain contexts, a phenomenon referred to as "choking." For example, research has demonstrated that offering people high rewards, which mimicked a high-stakes situation, resulted in greater errors on a variety of both motor and cognitive tasks (Ariely, Gneezy, Loewenstein, & Mazar, 2009). These deficits were interpreted as resulting from individuals perceiving the high reward state as a stressful opportunity, which in turn yielded states of physiological arousal maladaptive to task performance.

More recently, this concept of "choking" has been demonstrated within the domain of reward-motivated memory encoding. Callan and Schweighofer (2008) investigated whether reward's influence on memory was mediated by individual's anxiety about earning the reward. The authors found that reward motivation only benefited memory performance when individual levels of anxiety were reported as low. Murty, LaBar, Hamilton, and Adcock (2011) utilized a complementary approach to investigate this phenomenon by measuring individual's physiological arousal during reward-motivated memory. Similar to the prior study, the authors found that increased physiological arousal, a putative marker of anxiety, during reward motivation negatively predicted memory performance. Furthermore, participants that showed high arousal responses to reward incentives performed worse on rewarded versus non-reward conditions. These findings suggest that the benefits of reward motivation on memory vary across individuals and may be specific to low arousal/stress contexts.

To more directly test the relationship between aversive behavioral contexts and motivated memory, researchers have begun to investigate encoding in the context of punishment. These lines of research have investigated how negative reinforcers, such as irritating shocks or mildly painful thermal probes, influence encoding. These studies have demonstrated that punishment motivation enhances very simple forms of memory, but impairs more flexible and integrative forms of memory. For example, a study tested differences in reward and punishment motivation on spatial memory in a virtual-reality environment (Murty et al., 2011). Critically, successful performance on this task required the formation of flexible memories, which could integrate disparate features of the surrounding environment. Within this paradigm, reward motivation enhanced performance, while punishment motivation impaired performance. However, other studies have demonstrated that shock incentives enhance simple forms of memory, such as scene recognition (Murty et al., 2011; Schwarze, Bingel, & Sommer, 2012).

In an elegant study performed by Bauch, Rausch, and Bunzeck (2014), the researchers showed that painful reinforcers enhanced simple forms of memory but impaired more complex forms of memory within the same group of individuals. The authors observed that increasing threat of receiving a painful thermal probe resulted in better familiarity-based memory, which relies on simple item-based representations devoid of any contextual representations, but worse recollection-based memory, which contains details about the relationships amongst multiple features of an episode.

Neuroimaging studies have begun to isolate how different motivational incentives may result in different memory outcomes: namely, by engaging discrete targets in the MTL during encoding. As detailed above, many studies of reward motivation have revealed that memory enhancements are predicted by interactions between the VTA and hippocampus. Critically, these systems are known to support the encoding of integrative representations of memoranda (Davachi, 2006; Ranganath, 2010; Shohamy & Wagner, 2008). Interestingly, hippocampal activation is reduced during states of reward-evoked anxiety (Callan & Schweighofer, 2008) or increasing threat (Bauch et al., 2014; Forkmann et al., 2013). In states of punishment motivation, encoding-related activation has been observed in the amygdala and cortical MTL (Bauch et al., 2014; Murty, Labar, & Adcock, 2012; Schwarze et al., 2012). For example, Murty and colleagues (2012) showed that when individuals are motivated to encode scenes by the threat of shock, successful encoding is predicted by amygdala activation as well as amygdala-cortical MTL connectivity.

The neuroimaging findings dovetail well with the behavioral characterization of punishment motivation: cortical-MTL interactions are thought to support item-based representations in memory, as opposed to richer representations of both item and context supported by hippocampal activity. Thus, the resultant influence of motivation on memory may be determined by a host of factors, including the physiological response of an individual to the incentive as well as the neuromodulatory systems and MTL targets engaged during encoding. Further, negative affect during motivated encoding may shift encoding from hippocampus toward cortical-MTL pathways and lead to more sparse memory representations.

Summary: Motivation and Memory Encoding

In sum, the influence of motivational incentives on memory encoding is complex. Our present knowledge indicates that the impact of motivational incentives on memory encoding depends on three key factors: (1) incentive valence (reward or punishment), (2) the physiological response an individual has to the incentive, and (3) the neural substrates engaged during motivated encoding. Monetary reward motivation generally improves memory outcomes and engages the VTA and hippocampus during motivated encoding. However, this may change depending on an individual's response to the monetary reward incentive. If the reward causes an anxiety/stress response, then individuals tend to "choke" under pressure, perform worse under high incentives, and engage a distinct set of neural substrates – including the amygdala and cortical MTL – during encoding. This response parallels what is observed under punishment motivation, which typically enhances simple memories (e.g., familiarity), but impairs complex memories (e.g., recollection) that are thought to rely on the MTL. Going forward, differential responses to different types of motivational incentives should be accounted for and future work should explore the phenomenon of why identical incentives (e.g., money) may have dramatically distinct effects in different contexts or sub-populations of individuals.

MOTIVATION INFLUENCES MEMORY CONSOLIDATION

While the majority of studies have investigated the role of reward motivation on encoding-related processes (detailed above), motivation further supports memory by facilitating memory consolidation. Consolidation refers to the sequelae of events that occur after encoding that stabilize memory representations. These processes range in scale from cellular processes that strengthen experience-dependent plasticity in newly formed synapses, such as LTP, to broader systems-level processes that distribute memory representations throughout the cortex (Dudai, Karni, & Born, 2015). These processes result in memory representations that are resistant to the natural decay that is typically associated with forgetting. Thus, a hallmark measure of memory consolidation is that memory manipulations affect delayed, but not immediate memory tests, indicating the memory has been consolidated into long-term memory storage. Critically, animal and human research has shown that mesolimbic engagement and reward motivation can facilitate memory consolidation. In the next sections, we review animal and human literature demonstrating that reward motivation supports the consolidation of information via engagement of the mesolimbic system.

Mesolimbic Engagement and Memory Consolidation

Early support for the facilitation of consolidation via reward motivation emerged from animal work investigating downstream consequences of mesolimbic engagement during encoding. These early studies demonstrated that manipulating mesolimbic activation via drug administration influenced learning on delayed, but not immediate, assays of memory (Wang & Morris, 2010). Early work investigating hippocampal LTP demonstrated that application of a dopamine agonist, which enhances dopaminergic activation, facilitated markers of cellular consolidation, that is, late LTP (Huang & Kandel, 1995). Critically, increased dopaminergic activation did not influence early markers of LTP, suggesting that events following encoding further support memory stabilization.

These findings were further explored in a series of studies investigating memory performance while manipulating dopaminergic modulation during encoding. These studies demonstrated that administering dopamine antagonists (which block dopamine activation) during encoding, impaired performance on delayed tests of memory, but did not influence immediate tests of memory (reviewed by Wang & Morris, 2010). The fact that increasing dopamine activity facilitated consolidation, and decreasing dopamine activity impaired consolidation, provides strong initial support that mesolimbic activation helps to solidify long-term encoded memories, a hallmark of memory consolidation. In sum, dopamine can influence consolidation prior to and after encoding. As a result, the impact of dopamine is at times evident at the level of both encoding and consolidation, solely encoding, or solely consolidation. Future research should aim to elucidate the specific circumstances in which the impact of dopamine is evident at the level of encoding, but not consolidation, and vice versa.

Effects of Reward Motivation on Memory Consolidation

While the findings described above demonstrate a prominent role for mesolimbic activation in memory consolidation, they did not directly test whether reward motivation facilitates learning by acting on consolidation mechanisms. Rodent studies have recently demonstrated that motivation facilitates consolidation via mesolimbic activation. For example, Salvetti, Morris, and Wang (2014) tested rodents on a spatial navigation task, which was followed by either rewarding or neutral events. Critically, post-encoding introduction of reward enhanced performance on the spatial navigation task at a delayed memory test. Relatedly, previous work showed post-encoding memory enhancements by arousing stimuli (such as reward or novelty) are disrupted by dopamine blockade. These findings provide a critical link between motivation, mesolimbic activation, and facilitation of memory via consolidation.

Recent research in humans has paralleled rodent findings by manipulating reward motivation during encoding and assessing memory at immediate and delayed tests. A seminal study demonstrated that rewarding individuals for learning trivia information had no effect on immediate tests of memory (Murayama & Kuhbandner, 2011). When memory was tested at a 24-hour delay, however, motivation significantly enhanced memory, suggesting that post-encoding consolidation mechanisms support facilitation of memory by reward. Furthermore, studies have shown that rewarding events that take place after encoding enhance motivated memory on delayed, but not immediate, tests (Braun, Vail, Wimmer, & Shohamy, 2014; Murayama & Kitagami, 2014; Patil, Murty, Dunsmoor, Phelps, & Davachi, Under-revision). Finally, a recent human pharmacological study demonstrated that facilitation of memory consolidation is dependent on mesolimbic engagement during consolidation (Feld, Besedovsky, Kaida, Münte, & Born, 2014). Specifically, the authors demonstrated that the delayed memory benefits of reward motivation are abolished when individuals are administered dopamine antagonists post-encoding. These findings suggest that similar mechanisms may be guiding reward-motivated memory consolidation across species.

Effects of Reward Motivation on Neural Mechanisms of Consolidation

Results from both rodent neurophysiology studies and human neuroimaging studies have begun to unpack the mechanisms guiding reward's influence on memory consolidation. These studies have provided evidence that reward motivation promotes systems-level consolidation, a process by which events originally encoded in the hippocampus are "replayed" (meaning the neural traces are reactivated following initial activation during encoding) during post-encoding rest to distribute memories throughout the brain. In animal models, patterns of VTA activation and hippocampal activation that occur during rewarding events "replay" more often than activation patterns that occur during non-rewarded events (Gomperts, Kloosterman, & Wilson, 2015; Singer & Frank, 2009; Valdés, McNaughton, & Fellous, 2015). The higher rates of "replay" for rewarding events are thought to enhance the consolidation for these events.

Recent human neuroimaging techniques have begun to investigate "replay"-like events by looking at shifts in connectivity or reactivation of stimuli during periods of post-encoding rest (Gruber, Ritchey, Wang, Doss, & Ranganath, 2016; Murty, Tompary, Adcock, & Davachi, 2016). Using these techniques, post-encoding shifts in connectivity between the VTA, hippocampus, and sensory cortex have been shown to predict the benefits of reward motivation on memory. Together rodent and human studies indicate that reward motivation may increase the "replay" of rewarding experience to increase their durability in long-term memory.

Summary: Motivation and Memory Consolidation

In sum, motivation may facilitate memory performance, in part by facilitating memory consolidation and stabilization. Behaviorally, reward motivation has stronger effects on memory tested at delay, with only modest or null effects on memory tested immediately. Pharmacological evidence, in both rodents and humans, has associated reward-motivated consolidation with mesolimbic activation as (1) post-encoding mesolimbic engagement can enhance consolidation and (2) blockade of dopaminergic activation during encoding impedes memory stabilization. One potential mechanism by which reward may be supporting consolidation is by reactivating memories of rewarding events, which results in distribution of memory representations throughout cortex. In future studies, the relationship between reward motivation's influence on encoding and later consolidation should be examined. For example, how do enhancements in VTA-hippocampal connectivity during encoding relate to measures of memory consolidation and/or replay of rewarding events? Finally, the effect of motivation on memory consolidation in domains outside of reward motivation remains to be tested.

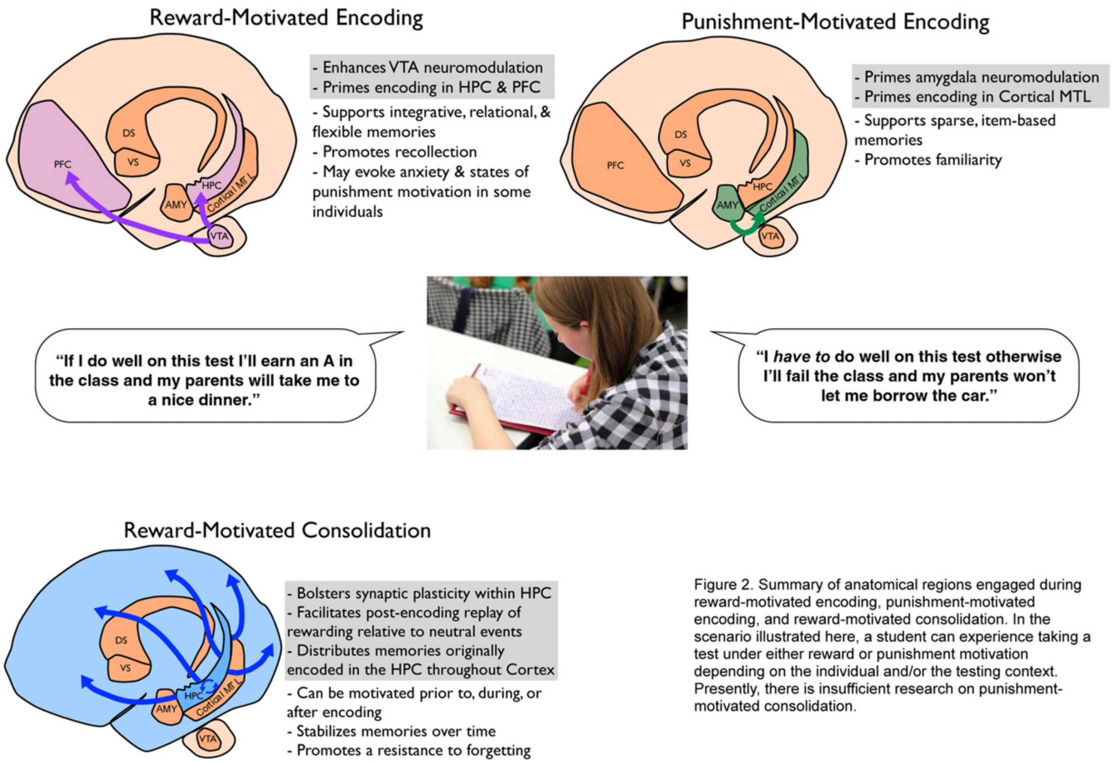
MOTIVATED MEMORY: IMPLICATIONS FOR EDUCATION

Thus far, we have reviewed findings across animal and human research investigating the influence of motivation on memory. These studies provide evidence that motivation promotes engagement of mesolimbic dopamine systems, which results in long-lasting influences on memory. We highlight two mechanisms by which motivation facilitates memory by (1) enriching encoding and (2) bolstering consolidation (see Fig. 2). Together, these literatures provide the foundation for investigations of how basic research can be translated to boost academic achievement. Below, we discuss potential implications for neuroscience-motivated memory research in educational contexts.

In regard to reward-motivated encoding, research demonstrates that reward incentives engage mesolimbic regions to support hippocampus-dependent memory encoding. The traditional focus on incentivizing memory in educational contexts has been on memory retrieval, that is, performance-based testing. The reviewed findings suggest that incentivizing encoding, as opposed to memory testing, can foster states of enriched learning. However, the majority of reviewed studies used monetary rewards to incentivize learning. The implementation of monetary rewards may not be tractable in educational contexts. Emerging research demonstrates that intrinsically rewarding incentives, such as a smiling face or curiosity, can similarly engage mesolimbic circuitry and promote enhanced learning. Capitalizing on these intrinsic incentives to improve learning in the classroom holds great promise to increase educational outcomes.

More recently, other behavioral contexts that facilitate mesolimbic engagement, such as the more active forms of learning and novelty, have also been shown to facilitate mesolimbic-hippocampal interactions during learning (Murty, DuBrow, & Davachi, 2015; Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011; Wittmann, Bunzeck, Dolan, & Düzel, 2007) and may be readily introduced into the classroom. Future pedagogical research could introduce incentive structures into curriculum to examine if these result in enrichment of student's academic experiences and performance. Particularly, these interventions need to focus on incentivizing learning as opposed to testing.

Critically, neuroscience research has demonstrated that incentivizing learning does not uniformly enhance memory. Instead, different motivational states engage discrete learning systems, which has downstream consequences on stored memories. When incentives are viewed positively, motivation facilitates VTA engagement and encoding in the hippocampus. Critically, hippocampus-dependent memories, which are highly contextualized containing details about multiple features of an experience and the relationships amongst them, may be the most ideal representations to foster in academic settings. These types of memories not only support



Reward-Motivated Encoding

- Enhances VTA neuromodulation
- Primes encoding in HPC & PFC
- Supports integrative, relational, & flexible memories
- Promotes recollection
- May evoke anxiety & states of punishment motivation in some individuals

Punishment-Motivated Encoding

- Primes amygdala neuromodulation
- Primes encoding in Cortical MTL
- Supports sparse, item-based memories
- Promotes familiarity

"If I do well on this test I'll earn an A in the class and my parents will take me to a nice dinner."

"I *have to* do well on this test otherwise I'll fail the class and my parents won't let me borrow the car."

Reward-Motivated Consolidation

- Bolsters synaptic plasticity within HPC
- Facilitates post-encoding replay of rewarding relative to neutral events
- Distributes memories originally encoded in the HPC throughout Cortex
- Can be motivated prior to, during, or after encoding
- Stabilizes memories over time
- Promotes a resistance to forgetting

Figure 2. Summary of anatomical regions engaged during reward-motivated encoding, punishment-motivated encoding, and reward-motivated consolidation. In the scenario illustrated here, a student can experience taking a test under either reward or punishment motivation depending on the individual and/or the testing context. Presently, there is insufficient research on punishment-motivated consolidation.

Fig. 2. Summary of Motivation's Influence on Memory Encoding and Consolidation.

vivid, associative memory retrieval (Yonelinas, 2002), but they also track future planning (Schacter, Addis, & Buckner, 2007), imagination and creativity (Buckner, 2010), emergence of conceptual knowledge (Kumaran, Summerfield, Hassabis, & Maguire, 2009), and generalization of learned information into novel domains (Kumaran & McClelland, 2012; Shohamy & Wagner, 2008; Wimmer & Shohamy, 2012).

Importantly, incentives, particularly monetary rewards, can often be viewed as aversive or stressful. In these aversive contexts, motivation fosters engagement of the amygdala and encoding within cortical MTL. These learning states support relatively sparse, inflexible memories. This motivational state may allow a student to perform well on a test of item-based knowledge, but it does not support the broader representations of knowledge that are most amenable to long-term educational goals. Thus, educational settings need to emphasize the fostering of environments by which motivation can best enhance learning: that is, ensuring motivational incentives evoke positive affect as opposed to stress. Whether an incentive induces positive affect or stress has been shown to vary across individuals, which has important implications for classroom settings. Namely, an individually titrated approach to education may be most beneficial for students. Importantly, it cannot be assumed that all incentives will have the same effect on all students. This may increase the burden on educators, but holds promise to ultimately significantly improve individual learning and educational outcomes.

Finally, motivation has been shown to support memory stability by supporting mechanisms of post-encoding consolidation. By engendering both cellular- and systems-level processes, consolidation can transform weakly encoded memories into strong, durable memories. Specifically, these consolidation processes are thought to distribute memories originally encoded in the MTL broadly throughout the cortex, which is proposed to greatly reduce susceptibility to forgetting. Fostering consolidation, thus, offers a means to ensure that information learned within a classroom persists for months to years.

One intervention that could facilitate consolidation in an academic setting is the introduction of positive or rewarding events throughout the course of a school day. In line with this, a recent study in an elementary school showed that introducing a novel learning experience, which theoretically engaged mesolimbic reward systems, resulted in better memory for unrelated information learned throughout the day (Ballarini, Martínez, Díaz Perez, Moncada, & Viola, 2013). Another intervention would be to restructure school days to include periods of rest and/or naps; indeed recent research shows that individuals have improved performance after sleep on a variety of tasks including memory, vocabulary, and motor imagery learning (Feld & Diekelmann, 2015). These findings are consistent with animal research which shows that mechanisms of consolidation are most prominent during periods of awake rest and sleep (Dudai et al., 2015; Rasch & Born, 2013). By introducing breaks throughout the school day, there may be improved efficacy in the retention of information learned in the classroom.

Neuroscience research has demonstrated that manipulating an individual's motivational state during and after learning is a powerful tool to facilitate memory. A broad array of interventions, centered on engagement of mesolimbic dopamine systems, could be implemented to translate these findings into educational contexts. Similarly, research on motivational constructs from educational psychology could kindle new domains of research for the neuroscience community.

Together, interactive collaborations between both neuroscience and education researchers would yield fruitful avenues of research and opportunities for novel interventions to harness basic science in service of academic achievement. Indeed pioneering work merging these fields has already begun to examine a variety of topics, mainly focused on manipulating retrieval, including the following examples: erroneous information and feedback effects on learning (Dunlosky, Rawson, Marsh, Nathan, & Willingham, 2013; Marsh, Fazio, & Goswick, 2012; Marsh, Lozito, Umanath, Bjork, & Bjork, 2012), how metacognition, feedback, and errors impact learning (Koriat & Goldsmith, 1996), testing effects on learning (for review, see Roediger & Butler, 2011), goal orientation and learning (Grant & Dweck, 2003; Smiley & Dweck, 1994), and how anxiety, stereotype threat, and stress impact learning (for review, see Inzlicht & Schmader, 2012). This initial, elegant work bridging the fields of cognitive neuroscience and education makes it the ideal time to conduct studies examining how research on motivated memory can be leveraged to impact educational outcomes.

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NEUROBIOLOGY OF EFFORT AND THE ROLE OF MESOLIMBIC DOPAMINE

John D. Salamone and Mercè Correa

ABSTRACT

Classical definitions of motivation typically involve two main components: direction and activation. Motivated behavior is directed toward or away from particular stimuli (i.e., appetitive and aversive motivation). Furthermore, activational aspects of motivation refer to the observation that motivated behavior is characterized by substantial activity, vigor, persistence, and exertion of effort in both the initiation and maintenance of behavior. Although separate neural systems direct organisms toward distinct motivational stimuli (e.g., food, water, sex), there appears to be a common circuitry regulating behavioral activation and the exertion of effort. Mesolimbic dopamine is one of the brain systems mediating activational aspects of motivation and exertion of effort. This system integrates aspects of motivation and motor control functions involved in the instigation of action. Research on the neurobiology of effort has contributed to our understanding of the pathophysiology of neurological and psychiatric disorders that are characterized by motivational dysfunction.

Keywords: Anergia; behavioral activation; depression; dopamine; effort; nucleus accumbens

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MOTIVATION: HISTORICAL BACKGROUND

Psychological constructs such as emotion, learning, and motivation are also commonly employed in neuroscience because of their explanatory value for integrating knowledge about the functions of neural circuits. Motivation is one of those constructs that is widely employed in both psychology and neuroscience, and as such has been defined in several different ways and discussed in many different contexts. As is the case with many psychological concepts, the discussion of motivation had its origins in philosophy. The German philosopher Schopenhauer (1999) considered the factors involved in motivational causation, and discussed how organisms must be in a position to "choose, seize, and even seek out the means of satisfaction." The modern psychological sciences emerged from both philosophy and physiology, and motivation was a key area of interest from the very beginning. Wilhelm Wundt and William James were early psychologists who included motivation (discussed as "will" or "volition," or in relation to goal seeking) as a subject in their academic textbooks (Elliot & Fryer, 2008). In the mid-20th century, while behaviorists such as B. F. Skinner (1953) did not emphasize motivation or other psychological constructs, neobehaviorists such as Hull (1943) and Spence (1956) employed motivational concepts such as drive and incentive to explain aspects of behavior. Today, both the psychology and neuroscience literatures are rich with the discussion of motivational theory and research.

DEFINITIONS OF MOTIVATION AND DIRECTIONAL ASPECTS

As stated above, there have been several different definitions of motivation. Young (1961) defined motivation as "the process of arousing actions, sustaining the activity in progress, and regulating the pattern of activity." According to a more recent definition (Salamone, 1992), motivation is "the set of processes through which organisms regulate the probability, proximity and availability of stimuli." Generally speaking, the modern psychological construct of motivation refers to the behaviorally relevant processes that enable organisms to regulate both their external and internal environment (Salamone, 2010). Furthermore, despite the fact that one can define motivation by using terms that make it distinct from other concepts or constructs, it should be recognized that at some point one must do more than define motivation, but also must consider its relation to other functions. Unfortunately, the neural representation of behavioral functions or psychological constructs does not involve dotted lines or box-and-arrow diagrams that neatly place core psychological functions into distinct neural systems without any overlap (Salamone, 2010; Salamone, Correa, Farrar, & Mingote, 2007). Thus, when discussing motivation, it is important to consider the relation between motivational processes and other important concepts such as homeostasis, allostasis, emotion, cognition, learning, reinforcement, and sensation. Furthermore, though it is often overlooked, it is necessary to consider the fundamental relation between motivational and motor functions. Motivation is not a process that merely refers to internal desires or states; rather it is a process that is fundamentally linked to action, which ultimately means that there also is considerable overlap between the neural regulation of motivation and movement (see next section).

Psychological constructs such as motivation continue to be employed in the literature because they are useful. In the case of motivation, its primary utility is that it offers a convenient summary of observable features of behavior, and provides a conceptual structure that is useful for organizing the findings of many experiments. It is often emphasized that behavior is "goal directed," and this aspect of behavior is sometimes referred to as the directional aspect of motivation. The behavior of organisms is directed toward or away from particular stimuli (e.g., food), as well as the activities that involve direct interaction with those stimuli (e.g., eating). Thus, organisms seek some stimulus conditions (i.e., appetitive stimuli such as food, water, and sex) and avoid others (i.e., aversive conditions such as pain, stressful stimuli, discomfort). Moreover, they can do so both actively (e.g., foraging for food) and passively (freezing in response to aversive stimuli).

Because organisms do not always have easy and direct access to motivationally relevant stimuli, motivated behavior typically takes place in phases. At the terminal end of the sequence of behavior, there is a direct interaction with the goal stimulus, which is commonly referred to as the consummatory phase. The word "consummatory" is often associated with Craig (1918), who conducted seminal studies in the field of animal behavior. However, this term does not actually refer to "consumption," but rather to "consummation." Consummation is a word of French/Latin origin, which means "to complete" or "to finish." In addition, because motivational stimuli usually are available at some physical or psychological distance from the organism, the only way to gain access to these stimuli is to engage in a pattern of behavior that closes this difference by bringing the organism to the stimulus, or delivering the stimulus to the organism by making its occurrence more likely. This phase of motivated behavior often is referred to as "appetitive," "preparatory," or "instrumental" (Blackburn, Phillips, & Fibiger, 1989; Craig, 1918; Salamone, 1992). The word instrumental was suggested for this specific purpose (Salamone & Correa, 2012; Salamone, 1992) because it is equally applicable to both approach and avoidance behavior, it fits the meaning of the term (i.e., serving as an instrument or means in pursuing an aim), and also because the term already is widely used in psychology (i.e., instrumental behavior or conditioning is a commonly used term).

BEHAVIORAL ACTIVATION, EFFORT, AND THE OVERLAP BETWEEN MOTIVATIONAL AND MOTOR FUNCTIONS

As well as being directed toward or away from particular stimuli or conditions, another fundamental feature of motivated behavior is that it has "activational" aspects (Salamone, 1988, 1992; Salamone & Correa, 2002, 2012). Motivated behavior is often characterized by a high degree of activity, vigor, or persistence. These activational aspects of motivation can be highly adaptive because when engaged, they enable animals to exert effort to gain access to the motivational stimulus. Organisms are typically separated from motivationally relevant stimuli by long distances, or by obstacles such as work-related response costs (Salamone, 1988, 1992; Salamone & Correa, 2012). Thus, engaging in instrumental behavior to obtain access to these stimuli typically involves work. Animals will forage in naturalistic settings, run in mazes in a laboratory, and lever press at high rates in operant boxes. Although the exertion of this effort can at times be relatively brief (e.g., a predator pouncing on its prey), under many circumstances it must be sustained over long periods of time (foraging over large areas of territory, maintaining persistent operant behavior across long sessions). Of course, humans also work hard to achieve goals, whether it involves walking several blocks to reach a snack machine, renovating a house, or working long hours to achieve a career goal. Organisms must allocate behavioral resources toward stimulus-seeking behavior, and motivated behavior is therefore characterized by considerable exertion of effort (i.e., speed, vigor, persistence, and high levels of work output).

The ability to work toward a goal by engaging in high-effort activity contributes to survival and evolutionary fitness. For these reasons, activational aspects of motivation are highly adaptive, and are fundamental to the overall construct of motivation. Early studies of the neural basis of motivation highlighted the importance of arousal and energy mobilization (Duffy, 1963). Hull (1943) and Spence (1956) used concepts such as drive and incentive to emphasize the energizing effects of motivational conditions on measures of instrumental performance (e.g., running speed in a maze). Cofer and Appley (1964) suggested that there was an "anticipation-invigoration mechanism" that could be instigated by conditioned stimuli that predict the availability of reinforcing stimuli, and which served to activate or invigorate instrumental behavior. Non-contingent scheduled presentation of primary motivational stimuli such as food can induce a number of different activities, including schedule-induced drinking (also known as polydipsia), licking, locomotion, and wheel running (Killeen, 1975, 1981; McCullough & Salamone, 1992a, 1992b; Robbins & Koob, 1980; Salamone, 1988; Wallace, Singer, Finlay, & Gibson, 1983). Several researchers have studied the impact of work requirements on the performance of an instrumental task, which ultimately helped to lay the groundwork for the development of economic models of operant behavior (Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). Ethologists also have employed similar concepts to explain aspects of animal behavior. Animals foraging in the wild often must expend considerable energy in order to obtain access to food, water, or nesting material (Salamone, 2010). Optimal foraging theory (Krebs, 1977) was proposed to account for the fact that the amount of effort or time expended to obtain these stimuli was an important determinant of foraging choice behavior. Pathological symptoms in humans such as fatigue, lassitude, anergia, and psychomotor slowing are common symptoms of depression, and also are present in people with a number of other psychiatric or neurological disorders (Salamone, Correa, Mingote, Weber, & Farrar, 2006).

As discussed above, it should be recognized that motivational processes do not operate in isolation, but instead should ultimately be considered as interacting with a variety of other psychological functions. For example, instrumental behavior is not only influenced by the motivational properties of reinforcing stimuli but also by learning mechanisms. Animals learn to engage in specific instrumental responses that are associated with particular reinforcing or punishing outcomes; effectively, organisms must learn which responses lead to which stimuli (Allison, 1993). Furthermore, behavioral activation frequently is instigated by conditioned stimuli that are associated with, and ultimately predict, motivational outcomes (Cofer & Appley, 1964; Salamone & Correa, 2012). In several ways, motivational functions are intertwined with cognitive, emotional, and other functions (Salamone, 2010). A thorough review of all these processes that interact with motivational functions is beyond the scope of the present chapter. However, for a discussion of the neurobiology of effort-related functions, it is critical to consider the relation between motivational and motor functions (Salamone, 1992, 2010). Of course, it axiomatic that every behavioral activity involves aspects of motor control. Food consumption involves organized patterns of motor activity, involving such acts as food handling, chewing, and swallowing. Nevertheless, it is clearly evident that activational aspects of motivation directly reflect features of motor output. There is a high degree of conceptual overlap between motor control and activational aspects of motivation, as well as functional overlap in terms of the neural systems involved and the behavioral measures obtained (Salamone, 1992, 2010).

Some examples are useful for illustrating the relation between activational aspects of motivation and motor control processes, which is seen in several behavioral situations. For example, food restriction can lead to a rat running faster in a maze. Does this phenomenon reflect processes that are motivational, motoric, or some combination of both? A common behavioral measure in rodents is locomotor activity, which clearly involves neural systems that regulate movement. Nevertheless, locomotor activity also is highly sensitive to motivational conditions. Increases in locomotor activity in rats can be induced by presentation of novel stimuli or food restriction, and scheduled presentation of small food pellets to a food deprived rat can generate excessive wheel running, or high levels of locomotor activity comparable to those seen after administration of major stimulants such as amphetamine (McCullough & Salamone, 1992a, 1992b). Furthermore, if an organism is presented with a work-related challenge while responding on an instrumental task, it often responds to that challenge by exerting greater effort. If a rat that has been trained to lever press on a continuous or fixed ratio (FR) 1 reinforcement schedule (1 lever press yields 1 food pellet) is then shifted to an operant schedule with a larger ratio requirement (e.g., FR5; 5 lever presses yield 1 food pellet), this increased work requirement creates an substantial upward pressure on response rates (Segovia, Correa, & Salamone, 2011; Segovia, Correa, Lennington, Conover, & Salamone, 2012). If the ratio requirement were to be increased further, up to levels such as FR60 or more, the rat would eventually display a radical shift in its response speed, emitting thousands of lever presses per half hour, with the vast majority of responses occurring at local rates considerably faster than once every 500 mseconds (Aberman & Salamone, 1999). Similarly, if a rat trained to run in a maze for food reinforcement is suddenly confronted with a barrier that blocks the maze arm, it quickly adjusts its behavior and leaps over the barrier to obtain the food (Salamone et al., 1994). If the barrier gets larger and larger over subsequent trials, the rat continues to adjust to the challenge and climb the barrier. Thus, the neural systems that regulate motor output appear to operate at the behest of those neural systems that are involved in motivation (Salamone, 2010). In some areas of the brain, motivational and motor systems circuits actually overlap (Mogenson, Jones, & Yim, 1980; Salamone, 1992, 2010; Salamone & Correa, 2002, 2012).

The examples listed above clearly demonstrate why it is important to emphasize the activational components of motivation. It is probably why Young (1963) defined motivation in terms of arousing actions and sustaining activity, and why Cofer and Appley (1964) considered it so necessary to suggest that there was a mechanism mediating the ability of conditioned stimuli to invigorate instrumental behavior. The examples listed above highlight the necessity of recognizing that there is overlap between aspects of motor control and motivational processes. Of course, the terms “motor control” and “motivation” do not have exactly the same meaning, and one can easily find functions that represent points of non-overlap. While initiation of osmotic thirst by activation of osmoreceptive cells is more related to directional aspects of motivation, Parkinsonian tremor is clearly more in the realm of movement control. Nevertheless, it is also evident that there is a fundamental overlap (Salamone, 2010). In this context, it is interesting to recognize that the English words movement and motivation both are ultimately derived from the Latin word *movere*, to move (i.e., *moti* is the past participle of *movere*).

THE ROLE OF MESOLIMBIC DOPAMINE IN BEHAVIORAL ACTIVATION AND EXERTION OF EFFORT

Behavioral neuroscientists have intensively studied the brain mechanisms thought to be involved in various aspects of motivation. Considerable research and theory points to the nucleus accumbens, which is part of the ventral striatum, as a point of functional overlap between brains systems involved in aspects of motivation and those involved in regulating motor output. In a seminal paper in this area, Mogenson et al. (1980) identified the nucleus accumbens as a brain area mediating the functional interaction between limbic brain areas involved in motivation, emotion, and cognition and basal ganglia regions involved in instigating behavioral output. Furthermore, the dopamine (DA) innervation of nucleus accumbens, which is part of the mesolimbic DA projection system, has been strongly implicated in activational aspects of motivation and effort-related processes. As described above, scheduled presentation of food pellets to food-restricted rats induces high levels of activities such as wheel running, excessive drinking, and locomotion. These environmental conditions are associated with substantial increases in accumbens DA release (McCullough & Salamone, 1992a, 1992b), and the schedule-induced activities can be blocked by low doses of DA antagonists (Salamone, 1986, 1988) and accumbens DA depletions (McCullough & Salamone, 1992a, 1992b; Robbins & Koob, 1980; Wallace et al., 1983). In contrast, interference with nucleus accumbens DA transmission, even at a level that can impair schedule-induced locomotor activity or lever pressing on operant schedules that have high-effort requirements, generally has no effect on food consumption (Baldo et al., 2002; Salamone, Mahan, & Rogers, 1993), little effect upon food-reinforced FR1 performance (Aberman & Salamone, 1999; McCullough, Cousins, & Salamone, 1993), and minimal actions upon the discrimination of reinforcement magnitude in maze choice tasks (Salamone et al., 1994). In addition, the effects of accumbens DA depletions on various operant procedures with high-ratio requirements are substantially different from those produced by prefeeding and appetite suppressant drugs (Aberman & Salamone, 1999; Randall et al., 2012, 2014; Salamone et al., 1991; Sink et al., 2008). Taken together, these findings demonstrate that fundamental aspects of food motivation are preserved after interference with accumbens DA transmission, indicating that nucleus accumbens DA depletion or antagonism can impair activational aspects of motivation while leaving directional aspects largely intact (Salamone, 1988, 2010; Salamone & Correa, 2002, 2009, 2012).

Considerable research also indicates that the effects of nucleus accumbens DA depletions on food-reinforced operant behavior depend greatly upon the kinetic or schedule requirements of the instrumental response. Depletions of DA in nucleus accumbens have little effect on total response output with rats responding on a FR1 schedule; their main impact in rats responding on this task is to produce an initial slowing of responding that does not closely resemble extinction (Aberman & Salamone, 1999;

Ishiwari et al., 2004; McCullough et al., 1993). Also, accumbens DA depletions have little effect on performance of variable interval schedules, such as variable interval 30, 60 or 120 seconds (Correa et al., 2002; Mingote, Weber, Ishiwari, Correa, & Salamone, 2005). Overall, nucleus accumbens DA depletions affect food-reinforced operant responding in rats in a manner that is directly related to the ratio requirement of the schedule (i.e., how many lever presses are required to receive a unit of reinforcement). Although FR1 lever pressing shows little sensitivity to the effects of accumbens DA depletions, schedules with higher ratio requirements (FR5 or 16 or 64 in some studies, or up to FR200 to 300 in other studies) are substantially impaired by interference with accumbens DA transmission (Aberman & Salamone, 1999; Ishiwari et al., 2004; Salamone et al., 2001). Nucleus accumbens DA depletions produce two effects on food-reinforced ratio performance: they reduce responding on schedules that have moderately high ratio requirements, and they dramatically suppress responding on schedules with very high ratio requirements (this is known as "ratio strain"). In summary, nucleus accumbens DA depletions appear to suppress the response enhancing effects of moderate size ratio requirements, and enhance the response suppressing effects of large ratios (Salamone, 2010; Salamone & Correa, 2002). Furthermore, it appears that the types of behaviors that are most sensitive to the disruptive effects of DA antagonism or depletions are vigorous instrumental behaviors that are elicited or sustained by conditioned stimuli (Salamone & Correa, 2012) (Fig. 1).

In discussing the effects of accumbens DA depletions on ratio lever pressing performance, there are several points worth emphasizing. First, the reduction of overall number of responses that occurs when there are low-to-moderate size ratio requirements is directly related to the baseline rate of responding; the higher the response rates, the greater the diminution of responding (Salamone et al., 1999, 2005). Second, the suppression of responding induced by DA depletion has two major components: (a) a slight decrease in the local rate of responding as reflected by alterations in the interresponse times (Mingote et al., 2005; Salamone et al., 1991), and (b) a very substantial increase in the number and duration of pauses in responding (Mingote et al., 2005; Salamone et al., 1991). In rats with DA depletions, lever pressing becomes more fragmented or "disengaged." Another feature of the effects of accumbens DA depletions on ratio performance is that the overall pattern of effects of DA depletion is completely different from the overall pattern of effects observed after prefeeding to reduce food motivation (Aberman & Salamone, 1999). Finally, the ratio strain that develops when tasks with very high ratio requirements are used

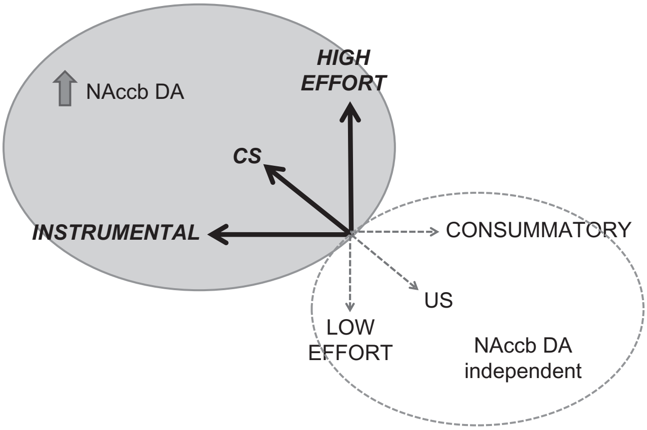

Fig. 1. This figure illustrates some of the factors that that are relevant for understanding the impact of DAergic manipulations on motivated behavior. Interference with accumbens DA transmission is very likely to disrupt vigorous or effortful instrumental behaviors that are instigated or supported by conditioned stimuli (Salamone & Correa, 2012). Consummatory behaviors such as food intake, which involves direct interaction with a primary motivational stimulus, and aversive behaviors induced by presentation of a primary aversive stimulus (e.g., escape), tend to be less easily disrupted by DAergic manipulations (see text for discussion). Although these factors are depicted as distinct dimensions, they also can interact in multiple ways. For example, instrumental behaviors are typically instigated by conditioned stimuli, and conditioned stimuli also have behaviorally activating properties.

(i.e., FR200–300) appears to be relatively independent of the baseline rate of responding, and actually more dependent upon the sheer size of the ratios (Salamone et al., 2001).

THE ROLE OF MESOLIMBIC DOPAMINE IN EFFORT-RELATED DECISION MAKING

In a complex environment, organisms can select from alternative sources of food and other motivationally relevant stimuli. Moreover, there are diverse paths for obtaining each of these stimuli, and each distinct trajectory can entail different response requirements related to time, work, and other parameters. Several behavioral paradigms have been developed that assess how animals allocate resources based upon analyses of reinforcement value and effort-related response costs. In general, tests of effort-based decision making involve offering animals a choice between a highly valued reinforcer (i.e., preferred) that can only be obtained by a high exertion of effort, versus a low-effort/low-reward option. As well as being involved in the exertion of effort in response to work-related obstacles or challenges, the results of multiple studies have demonstrated that nucleus accumbens DA also is involved effort-related decision making. In some studies, concurrent lever pressing chow feeding procedures have been employed. With this type of task, animals can choose between lever pressing on a FR or progressive ratio (PROG) schedule for a more preferred food reward (e.g., high carbohydrate operant pellets) versus approaching and consuming a less preferred food, such as common laboratory chow. Performance on these tasks is affected by the ratio requirements on the lever pressing component, thus demonstrating some degree of sensitivity to the work load placed on the operant schedule. With rats responding on a FR5 schedule for the preferred reward, untreated animals generally get most of their food from lever pressing (Nunes, Randall, Hart, et al., 2013; Salamone et al., 1991). Interference with DA transmission by systemic administration of low doses of DA antagonists, infusions of DA antagonists into nucleus accumbens, or accumbens DA depletions, all have been shown to shift choice behavior, decreasing lever pressing and substantially increasing chow intake (Cousins et al., 1994; Nowend, Arizzi, Carlson, & Salamone, 2001; Nunes, Randall, Hart, et al., 2013; Salamone et al., 1991; Sink et al., 2008). Reduced selection of the high-effort lever pressing option after interference with DA transmission also is seen when the lever pressing component of the choice task is a PROG schedule (Randall et al., 2012, 2014).

Another commonly used procedure is a T-maze task in which the two arms of the maze can have different reinforcement densities (e.g., 4 vs. 2 food pellets, or 4 vs. 0), and a work-related challenge is presented to the animal by having a large barrier blocking the arm with the higher reward density under some conditions. When there is no barrier present in the arm with the high reinforcement density, untreated rats generally prefer that arm, and neither DA antagonism nor accumbens DA depletions can affect preference for the arm with the higher reward density (Salamone et al., 1994). DA antagonism and accumbens DA depletions dramatically alter choice behavior when the high density arm (4 pellets) has the barrier in place, and the arm without the barrier contains an alternative food source (2 pellets); rats with impaired DA transmission show decreased choice of the high density arm (i.e., reduced barrier climbing), and increased choice of the low density arm without the barrier (Cousins et al., 1996; Salamone et al., 1994; Yohn, Santerre, et al., 2015; Yohn, Thompson, et al., 2015). Similar results are seen with mice (Pardo et al., 2012). Researchers also have developed lever pressing and T-maze versions of effort discounting tasks, and the results all point in the same direction, that is, interference with DA transmission alters effort-related choice behavior across a wide variety of tasks (Bardgett, Depenbrock, Downs, Points, & Green, 2009; Floresco, Tse, & Ghods-Sharifi, 2008; Hosking et al., 2015). These findings indicate that manipulations that affect nucleus accumbens DA transmission set constraints on effort-related choice behavior, biasing animals toward low-cost alternatives.

The effects of nucleus accumbens DA depletions on exertion of effort and effort-related choice behavior in food-motivated tasks do not appear to be dependent upon a general reduction of appetite for food, or an incapacity to respond, or the induction of severe motor impairments that limit response capacity (Pardo et al., 2012; Randall et al., 2012, 2014; Salamone et al., 1991; Sink et al., 2008; Yohn, Thompson, et al., 2015). For example, the effects of DA antagonism or depletion do not resemble the effects of reinforcer devaluation by prefeeding (Randall et al., 2012; Salamone et al., 1991) or appetite suppressant drugs (Randall et al., 2012, 2014; Sink et al., 2008). Taken together, this pattern of results does not appear to resemble the characteristics of either a reduction in directional aspects of food motivation (i.e., appetite) or a severe impairment in motor execution. Of course, there are brain areas at which dopaminergic manipulations can produce such effects. For examples, hypothalamic DA is involved in appetite, and ventrolateral neostriatal DA depletions can produce motor impairments in reaching, grasping, and forepaw usage during feeding, suppress feeding rate, and alter lever press duration (Salamone et al., 1993). Nevertheless, nucleus accumbens DA depletions produce more subtle, context dependent effects that appear to be related to functions that represent areas of overlap between motivation and motor control functions.

NUCLEUS ACCUMBENS DA AND THE BROADER NEURAL CIRCUITRY INVOLVED IN EFFORT-BASED CHOICE

Mesolimbic DA, while important for behavioral activation and effort-related processes, should be seen as a nodal point imbedded into a larger forebrain circuitry that includes other brain areas and neurotransmitters (Fig. 2). Several lines of evidence indicate that there is a distributed neural circuitry that regulates effort-based decision making, which includes basolateral amygdala, prefrontal/anterior cingulate cortex, and ventral pallidal GABA in addition to nucleus accumbens. These studies have involved anatomical, lesion, and pharmacology methods, as well as research using "disconnection methods" that involve combined contralateral manipulation of two different parts of the circuit (Farrar et al., 2008; Floresco & Ghods-Sharifi, 2007; Hauber & Sommer, 2009; Mingote et al., 2008; Salamone et al., 1994, 1997, 2007; Walton, Bannerman, Alterescu, & Rushworth, 2003). Within the accumbens, considerable research has demonstrated that DA interacts with the neuromodulator adenosine to regulate behavioral activity. Adenosine A_{2A} receptors are colocalized on striatal medium spiny neurons with DA D2 receptors, and a combination of neurochemical and behavioral evidence indicates that these receptors interact to regulate

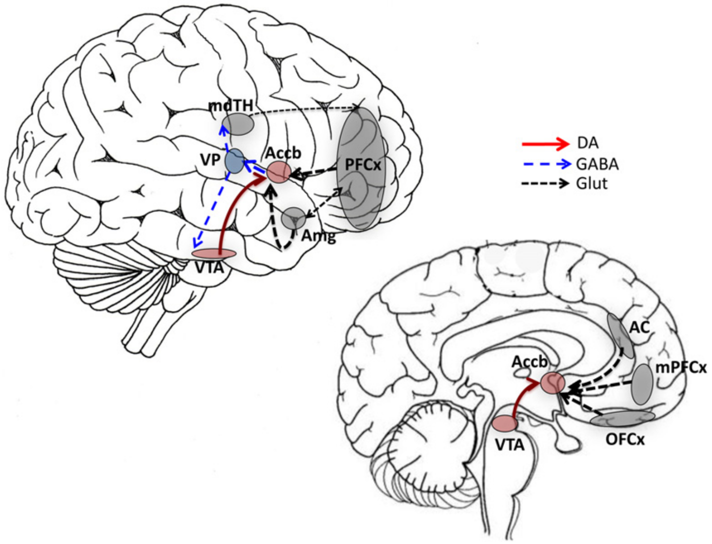

Fig. 2. Schematic Showing Anatomical Connections between Brain Structures Involved in Effort-Related Choice Behavior. *Notes*: Left – lateral view; Right – medial view. Accb – nucleus accumbens; PFCx – prefrontal cortex; AC – anterior cingulate cortex; OFCx – orbitofrontal cortex; VP – ventral pallidum; Amg – amygdala; MDth – medial dorsal thalamus; VTA – ventral tegmental area; DA – dopamine; GABA – gamma aminobutyric acid; Glut – glutamate.

effort-related decision making. Injections of adenosine A_{2A} antagonists, either systemically or locally into nucleus accumbens core, can reverse the effort-related effects of DA antagonists and restore near-normal patterns of behavior (Farrar et al., 2007, 2010; Mott et al., 2009; Nunes et al., 2010; Pardo et al., 2012; Salamone et al., 2009; Santerre et al., 2012; Worden et al., 2009). Conversely, injections of adenosine A_{2A} agonists directly into nucleus accumbens was shown to induce effects on effort-related choice that resemble those produced by DA depletion or antagonism (Font et al., 2008; Mingote et al., 2008). The adenosine A_{2A} antagonist MSX-3 increased lever pressing output in rats tested on the PROG/chow feeding choice procedure (Randall et al., 2012). Evidence also indicates that nucleus accumbens acetylcholine also is involved in effort-related decision making. Intra-accumbens injections of the muscarinic agonist pilocarpine decreased selection of the high-effort option in rats responding on the concurrent FR5/chow feeding choice procedure, which is consistent with previous studies indicating that striatal DA and acetylcholine interact (Nunes, Randall, Podurgiel Correa, & Salamone, 2013). Within the last few years, researchers have begun to characterize several components of the brain circuitry involved in effort-related decision-making processes (Fig. 2).

HUMAN STUDIES OF EFFORT-RELATED DECISION MAKING AND TRANSLATION INTO FORMAL ANIMAL MODELS OF PSYCHOPATHOLOGY

Basic animal research on the neural mechanisms underlying effort-related decision making has shed considerable light on the brain circuits and transmitters that regulate activational aspects of motivation for natural reinforcers. More recently, this research has been extended into lines of investigation that examine both normal and pathological aspects of human motivation. Ultimately, this has led to the development of formal animal models of effort-related psychopathologies.

Treadway, Buckholtz, Schwartzman, Lambert, and Zald (2009) developed the Effort-Expenditure for Rewards Task (EEfRT) in order to extend work on effort-related decision making to humans. With this task, people are given a choice on successive trials between a difficult (high-effort) choice and an easy (low-effort) option (Treadway et al., 2009). The high-effort choice required participants to make 100 button presses using the non-dominant little finger in 21 seconds, while the low-effort choice required 30 button presses with the index finger of the dominant hand within a 7-second window. Monetary reward was kept constant for selection of the low-effort option ($1.00), and selection of the high-effort option earned more money. One of the initial studies with this task (Wardle, Treadway, Mayo, Zald, & de Wit, 2011) examined the effects of the stimulant drug d-amphetamine, which enhances DA transmission by stimulating release and blocking uptake of DA, in healthy human volunteers. Amphetamine increased willingness to exert effort, as demonstrated by increased selection of the high-effort option. In another paper (Treadway, Bossaller et al., 2012), healthy human volunteers who were tested on the EEfRT task were also assessed using a dual-scan PET imaging protocol with [(18)F]fallypride and d-amphetamine to measure DA transmission. Correlational analyses demonstrated that individual differences in DA transmission in the left striatum and ventromedial prefrontal cortex were positively related to the willingness to expend greater effort for larger monetary rewards, especially when reward probability was low.

Within the last few years, there has been a dramatic increase in the number of studies focusing upon the use of tasks of effort-related decision making to characterize the motivational impairments seen in patients with various psychopathologies. Across multiple disorders, including depression, schizophrenia, Parkinson's disease, as well as patients with inflammatory challenges, there are numerous reports in the clinical literature of human pathologies involving psychomotor impairments or effort-related motivational symptoms. Motivational dysfunctions are commonly seen in medicine (Demyttenaere, De Fruyt, & Stahl, 2005), and motivational/psychomotor symptoms that are labeled in various ways (e.g., psychomotor retardation, fatigue, anergia, or lassitude) are frequently observed in patients with major depression and related disorders (Bella et al, 2010; Caligiuri et al., 2003; Demyttenaere et al., 2005; Fava et al., 2014; Salamone, Koychev, Correa, & McGuire, 2015; Salamone et al., 2006; Soskin, Holt, Sacco, & Fava, 2013; Stahl, 2002; Treadway & Zald, 2011). The severity of effort-related symptoms in people with major depression is correlated with impairments in social function, problems with employment, and treatment responsiveness (Stahl, 2002; Tylee, Gastpar, Lepine, & Mendlewicz, 1999). A correlational and factor analysis study of data from depressed patients identified a "lack of energy" factor that was related to problems such as low self-reported energy, increased fatigability, inability to work, and psychomotor retardation (Gullion & Rush, 1998). This factor was the one that loaded most strongly onto a second-order factor related general depression severity. As reviewed by Treadway and Zald (2011), depressed people can have fundamental impairments in exertion of effort during reward-seeking that do not depend simply upon reduced hedonic responsiveness to the primary motivational stimulus. Motivational symptoms in depression and other disorders are reported to be highly resistant to treatment (Fava et al., 2014; Stahl, 2002), which demonstrates that this is an important unmet need in psychiatry.

Within the last few years, researchers have employed human tasks of effort-related decision making to study effort-based dysfunctions in people with various types of disorders. Patients with major depression show reduced selection of high-effort alternatives (Treadway, Buckholtz, et al., 2012; Yang et al., 2014, 2015). Several reports involving multiple behavioral procedures in different laboratories have shown that schizophrenic patients also show reduced selection of high-effort choices, and tend to select low-effort alternatives when tested on choice tasks (Fervaha, Foussias, Agid, & Remington, 2013; Gold, Waltz, & Frank, 2015; Gold et al., 2013; Green & Horan, 2015; Green, Horan, Barch, & Gold, 2015; Hartmann et al., 2015). These results may be related to the negative symptoms, including motivational dysfunction, which are seen in people with schizophrenia. Parkinson's disease patients also showed reduced selection of high-effort alternatives compared to participants in the control group, and these deficits were significantly reduced when patients were being treated with dopaminergic medication (Chong et al., 2015).

In view of the fact that psychiatric symptoms related to deficits in behavioral activation and exertion of effort have been widely reported, it is important to develop formal animal models of effort-related pathologies. The rodent tasks described above are being adapted to study the effort-related effects of conditions associated with depression, and these procedures can be employed for the assessment of both novel and well established therapeutic agents. For example, recent studies have shown that conditions associated with depression in humans can alter effort-related choice behavior in rodents as evidenced by reduced selection of high-effort choices. Shafiei, Gray, Viau, and Floresco (2012) reported that restraint stress in rats shifted effort discounting, reducing selection of the high-effort alternative. Inflammatory conditions associated with depression also have been shown to reduce selection of high-effort choices (Nunes et al., 2014).

A number of recent studies have focused upon the motivational effects of tetrabenazine (TBZ). TBZ is an inhibitor of vesicular storage, which depletes brain DA. TBZ is used to treat Huntington's disease and other hyperkinetic movement disorders, but depressive symptoms are a major side effect (Chen, Ondo, Dashtipour, & Swope, 2012; Frank, 2009, 2010;

Guay, 2010). Recent studies have shown that low doses of TBZ can alter effort-related choice behavior as assessed by concurrent lever pressing/chow feeding choice procedures (Nunes, Randall, Podurgiel, et al., 2013; Randall et al., 2014; Yohn, Lopez-Cruz, Hutson, Correa, & Salamone, 2016), and the T-maze barrier choice task (Yohn, Santerre, et al., 2015; Yohn, Thompson, et al., 2015). TBZ decreased selection of high-effort lever pressing options such as FR and PROG schedules at low doses that did not alter relative preference for high carbohydrate pellets (the reinforcer for the high-effort option) versus chow intake (Nunes Randall, Podurgiel, et al., 2013), or high versus low concentrations of sucrose (Pardo, López-Cruz, Miguel, Salamone, & Correa, 2015), did not blunt appetitive taste reactivity to sucrose (Pardo et al., 2015), and did not produce effects similar to prefeeding or appetite suppressant drugs (Randall et al., 2012, 2014). In addition to being effective after systemic administration, TBZ also was shown to alter effort-based choice after local injections of the drug into nucleus accumbens core, but not into overlying medial dorsal striatum (Nunes, Randall, Hart, et al., 2013). Yohn, Thompson, et al. (2015) observed that TBZ could alter effort-related decision making in rats tested on the T-maze barrier task. TBZ decreased selection of the barrier arm that contained the high density of food reinforcement (4 pellets), and increased selection of the arm with 2 pellets but no barrier. In the low dose range that was tested (0.25–0.75 mg/kg), TBZ did not alter arm choice when there was no barrier in either arm, or when the arm with the barrier had 4 reinforcement pellets but the other arm had no pellets. Thus, TBZ did not decrease selection of the high-effort alternative (i.e., the barrier arm) because it disrupted sensitivity to reinforcement magnitude, preference based upon number of pellets, left/right discrimination, or reference memory, or because of a reduction in the ceiling number of barrier crossings or the induction of an absolute inability to climb the barrier (Yohn, Thompson, et al., 2015).

Several drugs have been evaluated for their ability to reverse the deficits in effort-related choice described above, including well-known antidepressants and other types of compounds. Bupropion (trade name Wellbutrin) is a widely prescribed antidepressant (Milea, Guelfucci, Bent-Ennakhil, Toumi, & Auray, 2010). Bupropion is an antagonist of catecholamine uptake, and this drug has been shown to occupy DA transporters in humans at doses that are clinically effective (Learned-Coughlin et al., 2003). Animal research has shown that bupropion also increases levels of extracellular DA and norepinephrine (NE) in rats as determined by microdialysis methods (Hudson, Lalies, & Silverstone, 2012;

Randall et al., 2015). In rats tested on the T-maze barrier choice task, bupropion fully reversed the effects of TBZ, as marked by an increase in selection of the barrier arm in TBZ-treated rats (Yohn, Thompson, et al., 2015). Bupropion also has been shown to reverse the effort-related effects of TBZ in rats tested on the FR5/chow feeding choice (Nunes Randall, Podurgiel, et al., 2013) and the PROG/chow feeding choice tasks (Randall et al., 2014). These findings are consistent with reports showing that blockade of DA uptake could increase progressive ratio choice lever pressing output (Sommer et al., 2014). Furthermore, these results are consistent with experiments showing that amphetamine enhanced selection of the high-effort alternative in humans responding the EEfRT test of effort-related decision making (Wardle et al., 2011). Because bupropion is effective as an antidepressant in humans, and has been reported to be able to reverse motivational dysfunction in depressed patients (Cooper, Tucker, & Papakostas, 2014), these results provide a validation of the hypothesis that tests of effort-related decision making in rodents can be used to assess some of the motivational effects of well-known or putative therapeutic agents (Salamone et al., 2015).

Although effort-related symptoms in humans are generally reported to be resistant to treatment, clinical studies indicate that catecholamine uptake inhibitors can be moderately efficacious for treating psychomotor retardation and fatigue symptoms of depression (Cooper et al., 2014; Pae et al., 2007; Rampello, Nicoletti, & Raffaele, 1991). Furthermore, evidence indicates that blockade of catecholamine uptake can be more effective than 5-HT uptake inhibition for treatment of motivational dysfunction in depressed patients (Cooper et al., 2014; Papakostas et al., 2006). For that reason, recent studies have compared the effects of monoamine uptake inhibitors with different selectivity profiles for their ability to reverse the effects of TBZ (Yohn et al., 2016). In rats tested on the concurrent FR5/chow feeding choice task, the effort-related effects of TBZ were attenuated by bupropion, an effect that was reversed by antagonism of either D1 or D2 family receptors. In addition to bupropion, the selective DA transport inhibitor GBR12909 was shown to attenuate the effort-related effects of TBZ. In contrast to the effects of DA uptake blockade, the 5-HT uptake inhibitor fluoxetine and the norepinephrine uptake inhibitor desipramine both failed to reverse the effects of TBZ. In fact, higher doses of these drugs, when given either alone or together with TBZ, resulted in further behavioral impairments (Yohn et al., 2016). Another recent study has reported that the catecholamine uptake inhibitor lisdexamfetamine (a prodrug of d-amphetamine) was able to reverse the effort-related effects of TBZ, while the 5-HT uptake blocker s-citalopram was not (Yohn et al., 2016). Thus, it appears that drugs that act upon DA transmission are relatively effective at reversing the effort-related effects of TBZ compared to drugs that act on 5-HT and norepinephrine. These findings suggest that drugs that enhance DA transmission may be effective at treating effort-related psychiatric symptoms in humans, although one must be cautious about possible side effects, including abuse liability.

Another class of drugs that has been assessed in animal models of effort-related symptoms is adenosine A_{2A} antagonists. These drugs have been shown to reverse the effort-related effects of TBZ in rats responding across multiple tasks (Nunes, Randall, Hart, et al., 2013; Randall et al., 2014; Yohn, Thompson, et al., 2015). These recent findings are consistent with previous research demonstrating that adenosine A_{2A} antagonists are able to reverse the effort-related actions of DA D2 receptor antagonists (Farrar et al., 2007; Mott et al., 2009; Nunes et al., 2010; Pardo et al., 2012; Salamone et al., 2009; Santerre et al., 2012; Worden et al., 2009). As shown in anatomical studies, adenosine A_{2A} receptors are co-localized with DA D2 family receptors on enkephalin-positive medium spiny neurons throughout the entire striatal complex, including the nucleus accumbens (Svenningsson, Le Moine, Fisone, & Fredholm, 1999). Thus, it appears that adenosine A_{2A} receptor antagonists, some of which are already available as antiparkinsonian drugs in humans, may be useful for the treatment of effort-related motivational symptoms (Nunes, Randall, Hart, et al., 2013; Randall et al., 2012, 2014; Salamone et al., 2015).

EDUCATIONAL IMPLICATIONS

In addition to being related to the study of the neural mechanisms involved in aspects of depression, the study of effort-related functions may also have educational implications. For example, stimulant drugs such as lisdexamfetamine (Vyvanse) and methylphenidate (Ritalin), which block DA uptake, have been shown to reverse the effort-related impairments induced by TBZ, and increase exertion of effort (Salamone, Yohn, Lopez Cruz, San Miguel, & Correa, 2016; Yohn et al., 2016). In rats performing on a task of cognitive effort-based decision making, the stimulant drug amphetamine increased selection of high-effort cognitive tasks (Cocker, Hosking, Benoit, & Winstanley, 2012). Furthermore, amphetamine has been shown to increase selection of high-effort choices in humans responding of tasks involving physical effort-based decision making (Wardle et al., 2011). It is worth noting that these drugs are most commonly used in humans for the treatment of attention deficit hyperactivity disorder (ADHD). The use of stimulants to treat educational impairments in people with ADHD is well documented (Brown, 2005). Although this effect is often viewed in terms of modulating attentional mechanisms that are necessary for learning, it also is true that stimulant medications can enhance performance by increasing self-motivation and task persistence (Brown, 2005; Modesto-Lowe, Chaplin, Soovajian, & Meyer, 2013).

CONCLUSIONS

As described above, multiple lines of evidence ranging from basic behavioral neuroscience studies and animal models to human clinical research indicates that brain DA systems participate in the regulation of aspects of motivation. Although DA systems are often miscast as mediating "reward" or subjective pleasure, the details of the research findings indicate that this traditional view is grossly oversimplified and inaccurate, and that the motivational functions of mesolimbic DA are much more related to behavioral activation and effort-related processes (Salamone & Correa, 2002, 2012). Of course, mesolimbic DA does not regulate these types of motivational functions in isolation, but rather, DA systems are part of a broader circuitry that includes limbic, prefronal, and pallidal structures, as well as multiple neurotransmitters (adenosine, acetylcholine, GABA). Continued research on the neurobiology of behavioral activation and effort-related processes will help to elucidate how brain mechanisms participate in the regulation of both natural and pathological features of motivation, and also how directional aspects of motivation that steer animals toward specific motivational stimuli can ultimately be translated into vigorous and persistent action.

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DISCLOSURE/CONFLICT OF INTEREST

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HORMONES AND AFFECT IN ADOLESCENT DECISION MAKING

Corinna Laube and Wouter van den Bos

ABSTRACT

Teenagers are typically described as impulsive and risk taking. Yet recent research shows that this observation does not hold in all contexts. Rather, adolescents show higher impulsivity and risk taking than children or adults in affective *contexts. Motivational and affective processes are therefore of particular interest when trying to understand typical adolescent behavior. Additionally, pubertal hormones are hypothesized to play a special role in adolescents' motivated decision making. However, evidence for the mechanisms underlying this relationship is sparse. In this chapter, we aim to integrate findings from human and animal studies in order to elucidate the specific impact of pubertal hormones on motivational processes in adolescence. Against this background, we critically discuss and reinterpret recent findings in psychology and neuroscience, speculate about underlying mechanisms, and suggest new approaches for future studies of adolescent behavior.*

Keywords: Adolescence; puberty; testosterone; risk taking; impulsivity; affect

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ADOLESCENCE AS A PERIOD OF MOTIVATED BEHAVIOR

> "Adolescence is practically synonymous in our culture with risk taking, emotional drama and all forms of outlandish behavior." (Friedman, 2014)

Adolescence describes the developmental phase between childhood and adulthood. It is characterized by a transition from dependence to independence, as well as by sexual maturation. The path to independence is associated with a process of major social re-orientation, in which the influence of parents becomes less pronounced and that of peers increases (Nelson, Leibenluft, McClure, & Pine, 2005; van den Bos, 2013). The start of adolescence is often defined by the onset of puberty, whereas its end is culturally defined: whenever an individual is considered to be an adult. Puberty covers a shorter time interval; it is the process of hormonal and physiological changes by which individuals reach sexual maturity and is found in most mammals (Spear, 2010).

One salient characteristic of adolescence is an increase in risky and impulsive behavior (Braams, van Duijvenvoorde, Peper, & Crone, 2015; O'Brien, Albert, Chein, & Steinberg, 2011; Steinberg et al., 2009). Social problems in adolescence such as drunk driving, suicide, and teenage pregnancy are often attributed to this increased risk taking and impulsivity (Dahl, 2004). Furthermore, risky behavior results in a significant increase in adolescents' visits to the emergency room (Steinberg, 2007) and to a 200% increase in the mortality rate among teenagers (Dahl, 2004).

Adolescence as a time of turbulence and excess is not a creation of modern society. Historical accounts of adolescent impetuosity go back as far as ancient Greece (300−600 BC), with typical teenage behaviors such as rashness, sexual excess, frivolity, drunkenness, and lack of self-control being portrayed in ancient Greek art (Harlow & Laurence, 2002). "Irrational" adolescent behavior has traditionally been attributed to "raging hormones" (Buchanan, Eccles, & Becker, 1992); more recently, neuroscientific methods have shown that teenagers' prefrontal cortex, an area involved in decision making and rationality, is not yet fully developed (Yurgelun-Todd, 2007). However, the latest scientific discoveries suggest that typical adolescent behavior has multiple interactive causes and may often be adaptive rather than irrational (Crone & Dahl, 2012; Dahl, 2004; Pfeifer & Allen, 2012). Besides the development of cognitive control, motivational processes also seem to play an important role in adolescent behavior (Crone & Dahl, 2012; Ernst, 2014; Somerville & Casey, 2010; Steinberg, 2008). It has been argued that these adolescent-specific changes in motivational processes afford both risks and opportunities (Blakemore & Robbins, 2012; Crone & Dahl, 2012).

The shift in attention to motivational processes has sparked renewed interest in the role of pubertal hormones in adolescent behavior. It is hypothesized that these hormones specifically impact motivational processes during this developmental phase, which in turn leads to increased risk taking and impulsive behavior, but also supports positive development in adolescence (Crone & Dahl, 2012). However, little is known about the mechanisms that mediate the relationship between hormones and changes in motivational processes during adolescence or how these changes in motivational processes may heighten adolescent risk taking and impulsivity.

In this chapter, we aim to integrate findings elucidating the specific impact of pubertal hormones on motivational processes in adolescence. First, we review findings from self-report and behavioral studies of adolescent decision making in order to better understand the changes that occur in motivational processes during this developmental period and how those changes relate to a specific subset of behaviors: risk taking and impulsivity. Next, we consider the role of hormones in pubertal development and how they relate to adolescent risk taking and impulsivity. Together, these findings suggest that pubertal hormones indeed have a sizeable influence on risky and impulsive behavior in adolescence, and that this effect is accompanied by context-dependent changes in motivational processing. To better understand the possible mechanisms by which pubertal hormones impact behavior, we turn to recent findings from neuroscience. Here, we focus on adolescent-specific changes in motivational brain systems and the potential impact of hormones on these systems. We conclude by deriving general educational implications and identifying directions for future research.

Note that we constrain adolescent behavior to *risk taking and impulsivity* given the fact that we currently find the most available evidence in these two domains. Finally, although we recognize that increased adolescent risk taking in the real world can be partly attributed to decreased parental control (Defoe, Dubas, Figner, & van Aken, 2015; Romer, 2010) and to developmental changes in cognitive skills, such as reasoning skills (Reyna & Brainerd, 2012), addressing these issues would go beyond the scope of this chapter. On an endocrinological level, we focus on testosterone, which is known to be associated with risky and impulsive behavior.

THE ROLE OF MOTIVATIONAL PROCESSES IN ADOLESCENT DECISION MAKING: FINDINGS FROM SELF-REPORT AND BEHAVIORAL STUDIES

Self-report measures indicate that impulsivity, sensation seeking, and consequently risk taking are elevated during adolescence. A common definition of impulsivity is the tendency to act without planning or considering potential consequences (e.g., "I like to stop and think things over before I do them" [reversed item]). Sensation seeking can be defined as the tendency to seek out experiences and situations that are novel, exciting, or rewarding; typical items are "I quite enjoy taking risks" or "Life with no danger in it would be too dull for me" (Harden & Tucker-Drob, 2011). Findings from behavioral and self-report studies indicate that impulsivity tends to show a linear decline as a function of age (Quinn & Harden, 2013; Steinberg, 2008; Steinberg et al., 2009; Vaidya, Latzman, Markon, & Watson, 2010; van den Bos, Rodriguez, Schweitzer, & McClure, 2015), whereas sensation seeking follows an inverted U-shape curve (Cauffman et al., 2010; Harden & Tucker-Drob, 2011; Romer & Hennessy, 2007; Steinberg, 2008). Harden and Tucker-Drob (2011) have replicated these developmental patterns of age trends in a longitudinal study with a sample of 7,640 adolescents. Impulsivity and sensation seeking can thus be regarded as distinct traits that are influenced by qualitatively different developmental processes in adolescence. Specifically, impulsivity is strongly associated with lack of cognitive control, whereas sensation seeking is thought to stem from sensitivity to motivational cues (Steinberg, 2007, 2008). Yet although the two constructs are distinct, they are both associated with developmental changes in risky behavior. For instance, a longitudinal study by Quinn and Harden (2013) showed that age-related changes in both impulsivity and, to a lesser extent, sensation seeking accounted for variability in substance use change. Specifically, individuals who showed slower declines in impulsivity and sensation seeking showed faster increases in substance use. This pattern of results suggests that adolescent behavior is the outcome of an interaction between distinct motivational forces and (limited) cognitive control, all of which are still under development.

Laboratory experiments have provided further insights into (1) the cognitive/affective processes involved in adolescent behavior and (2) the conditions under which this behavior tends to occur. It is important to note, however, that a recent meta-analysis of behavioral risk studies by Defoe et al. (2015) revealed a discrepancy between patterns of risk taking in the real world and adolescent behavior as studied in the laboratory. In contrast to many reports about real-world risk taking (Dahl, 2004; Willoughby, Good, Adachi, Hamza, & Tavernier, 2013), laboratory studies have not generally found risk-taking behavior to peak in adolescence: Although adolescents take more risks than adults, and early adolescents take more risks than mid-late adolescents, lab studies typically show no difference between early adolescents and children in terms of risk taking. One possible reason for this discrepancy is that the structure of the tasks used in laboratory studies does not match that of the real-world environment.

For instance, a common way to study risky decision making is to present simple gambles (wheels of fortune) that link outcomes of different magnitudes with different probabilities (see Ernst et al., 2004). In a study by Van Leijenhorst et al. (2010), participants were presented with choices between options with a high probability of a small reward (low-risk/low-reward) and options with a low probability of a large reward (high-risk/high-reward). Such tasks differ from the real world in several crucial ways. First, in the real world, the true probabilities are often unknown (Hertwig & Erev, 2009). Second, real-world adolescent risk taking is thought to occur mainly in arousing contexts. For example, the risk of fatal injury for a 16- or 17-year-old driver increases with the number of passengers (Chen, Baker, Braver, & Li, 2000). In the following, we review evidence from laboratory studies suggesting that adolescents indeed show more risk-taking behavior than either adults or children in experimental paradigms that involve arousing conditions, to which they are more sensitive.

Figner, Mackinlay, Wilkening, and Weber (2009) designed a dynamic risk-taking task, the Columbia Card Task, to study age differences in risk taking and underlying information use. In this task, participants are shown 32 cards face down on a computer screen. Each card indicates a gain (which is added to the trial payoff) or a loss. Players can turn over as many cards as they like until they encounter a loss card, which terminates the trial. The aim of the game is to score as many points as possible. Figner et al. (2009) implemented two conditions: one "hot" and one "cold" condition. In the hot condition, participants received immediate feedback and were allowed to make stepwise incremental decisions about turning over another card. In the cold condition, they had to make a single decision on the total number of cards to be turned over in each trial and received outcome feedback only at the very end of the game. Figner et al. (2009) argued that both receiving immediate feedback and deciding which card to turn over next trigger affective processes. They found that adolescents took more risks than children and adults in the hot condition, whereas risk taking was similar across all ages in the cold condition.

The Iowa gambling task is another dynamic risk-taking task that is frequently used to assess risk taking in the laboratory. It approximates real-life decision making under uncertainty (Bechara, Damasio, Damasio, & Anderson, 1994) – that is, the probabilities and outcomes are not described upfront but have to be learned during the task. Specifically, participants are presented with four decks of cards, each containing cards that reward or punish the player by adding or subtracting points or amounts of money from his or her account. Two of the decks lead to net increases over the course of repeated play (the advantageous decks); the other two lead to net losses (the disadvantageous decks). Cauffman et al. (2010) used a modified version of the Iowa Gambling Task to measure affective risk taking in a diverse sample of 901 individuals aged between 10 and 30 years. Adolescents increasingly played from the advantageous decks; this learned preference for the advantageous decks was interpreted as approach behavior, and displayed an inverted U-shape relation to age, peaking in mid- to late adolescence.

In the Balloon Analog Risk Task (BART; Lejuez et al., 2002), another "hot" laboratory risk-taking task, participants have to inflate a computerized balloon one pump at a time. They earn a monetary reward each time they pump the balloon but lose the entire reward if the balloon bursts. Consequently, larger rewards can be earned by taking more risks. Several recent studies using the BART have found a peak in risk-taking behavior in adolescents, relative to children and adults (Braams et al., 2015; van Duijvenvoorde et al., 2015); others have found no such peak in adolescence (see Defoe et al., 2015).

Finally, several studies have shown that the mere presence of peers increases adolescents' risk taking relative to adults' (Gardner & Steinberg, 2005; O'Brien et al., 2011). For instance, Gardner and Steinberg (2005) found that the presence of peers more than doubled the number of risks teenagers took in a video driving game. However, it had no effect at all on adults. Similarly, in a study with a delay discounting task, O'Brien et al. (2011) found that adolescents preferred more immediate rewards to later ones when in the presence of their peers. In this study, participants had to choose between a smaller sooner reward (e.g., $200 today) and a larger later reward (e.g., $1,000 in one year). Adolescents were more likely to choose the smaller sooner reward in the presence of peers than when alone. The presence of peers is hypothesized to be a highly arousing context for adolescents and this increased arousal is thought to change their behavior in a similar fashion as the arousing context provided by "hot" gambling games. It is also possible that adolescents in peer social contexts take risks in order to send social signals (Milchunas, Sala, & Lauenroth, 1988).

In conclusion, there is substantial evidence that adolescents show increased risk taking and impulsivity in laboratory studies *under arousing conditions*. Given that the cognitive components of the tasks administered are assumed to be stable across conditions, these findings suggest that there is something specific about how adolescents process the affective motivational components of the tasks. However, behavioral studies can provide only limited insights into the underlying mechanisms. In the next section, we argue that hormones play an important role in modulating the affective motivational processes involved in adolescent risk taking and impulsivity.

THE ROLE OF PUBERTAL HORMONES

The idea that the particularly pronounced changes in mood and behavior observed in adolescence result from biological factors such as a rapid change in hormone levels goes back to at least the early 1900s (Hall, 1904). This change in pubertal hormones is not specific to humans but is a cross-species phenomenon, and a variety of species show puberty-typical behaviors such as novelty seeking and increased peer interactions (Spear, 2000). Yet it remains unclear how pubertal hormones relate to increased risk taking and impulsivity in adolescence. Previous research has focused on age, rather than pubertal maturation, as a predictor of developmental changes in risk behavior. However, a handful of studies suggest a link between pubertal hormones and developmental changes in arousal, motivation, and emotion (Blakemore, Burnett, & Dahl, 2010; Crone & Dahl, 2012; Forbes & Dahl, 2010; Peper & Dahl, 2013; Steinberg, 2005). Before we review the relationship between hormones, specifically testosterone, and adolescent behavior, we briefly outline the mechanisms behind the hormonal changes seen in puberty.

Pubertal Development

Pubertal development is associated with a rapid rise in gonadal hormone release initiating development of secondary sexual characteristics, such as breast development in girls and pubertal hair growth, as well as other physiological changes, such as physical growth. The sex hormones regulating bodily changes are testosterone, oestradiol, and dehydroepiandrosterone (DHEA). The hormonal cascade initiating the release of these hormones from the gonads begins in the brain, and a feedback mechanism known as the hypothalamic–pituitary–gonadal (HPG) axis regulates endocrine function. Pubertal onset is associated with the activation of neurons located in the hypothalamus that secrete gonadotropin-releasing hormone (GnRH). GnRH then travels to the pituitary gland, where it regulates the synthesis and secretion of two pituitary gonadotropins: luteinizing hormone (LH) and follicle-stimulating hormone (FSH) (see Fig. 1). Released into the bloodstream, LH and FSH then jointly act to stimulate the production of gonadal steroid hormones, completing the process of egg and sperm development. The appearance of secondary sexual characteristics in peripheral tissues (e.g., breast development in girls and facial hair in boys) in turn leads to elevated levels of estrogen and progesterone.

How does the brain know when to activate the HPG axis and trigger puberty? Both internal and external cues provide information on the availability of necessary resources for successful reproduction. Internal cues

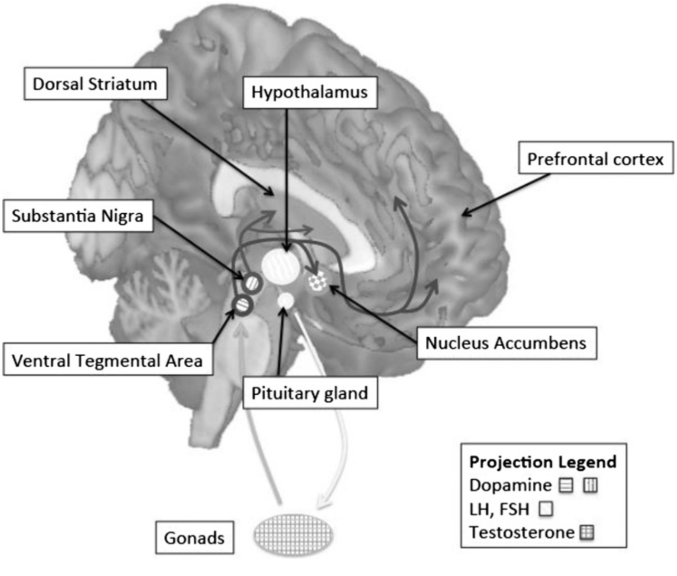

Fig. 1. Dopaminergic and Hormonal Pathways in the Brain.

include biological prerequisites for pregnancy, such as metabolic levels of insulin, glucose, and leptin that indicate somatic growth and metabolic fuel availability; lower body fat has been associated with delayed pubertal onset (Frisch, 1984). External cues include information on the availability of a suitable mate and food. Furthermore, females typically enter and move through adolescence more quickly than males (Savin-Williams & Weisfeld, 1989), suggesting biological sex as an important factor in pubertal timing. To conclude, the timing of pubertal onset should be viewed as a neurological rather than a gonadal event (Sisk & Zehr, 2005). That is, it is the nervous system that integrates different cues from the body and the environment and, as such, determines pubertal onset (Sisk & Zehr, 2005).

Pubertal Maturation Measures

Different methods are used to assess pubertal development. The indirect method of Tanner staging (Tanner, 1962) categorizes individuals along an ordinal puberty scale from 1 (no development) to 5 (adult development). These standardized categories capture visible secondary sexual characteristics such as breast or genital development and pubic hair growth. Tanner stages can be determined by physical exam conducted by a trained clinician or by self-report. Another common way of measuring external pubertal status is the Pubertal Developmental Scale (PDS) (Petersen, Crockett, Richards, & Boxer, 1988). Like the Tanner scale, the PDS asks adolescents about hair growth, skin changes, and growth spurts, with sex-specific items, such as menarche and breast development in females and genital growth and facial hair in males. The resulting composite puberty score reflects the effects of adrenal and gonadal hormones as well as growth hormones.

Shirtcliff, Dahl, and Pollak (2009) examined the interrelations of multiple indices of puberty and found that PDS scores are related to levels of basal hormones, such as testosterone in boys. However, even the best measure of external pubertal status captures less than half of the variability in basal hormones (Shirtcliff et al., 2009). Measuring hormone levels in saliva or blood can thus give important insights into pubertal maturation that are not available from overt physical measures alone. Given the variety of changes accompanying puberty, the best pubertal status measurement will depend on the issues being investigated.

The Influence of Testosterone on Adolescent Behavior

Vermeersch, T'Sjoen, Kaufman, and Vincke (2008) found a positive relationship between testosterone and risk taking in a sample of 301 adolescent boys, independent of age and pubertal development as measured by the Tanner scale. Interestingly, this effect was partly mediated by peer influence: boys with high levels of testosterone also had peers who were more involved in risky behaviors, which in turn influenced their own risk taking. This finding is in line with substantial evidence indicating that individual levels of testosterone also predict differences in risky behavior in *adults* (Booth, Johnson, & Granger, 1999; Campbell et al., 2010; Goudriaan et al., 2010; Rosenblitt, Soler, Johnson, & Quadagno, 2001; Stanton, Liening, & Schultheiss, 2011; Stenstrom, Saad, Nepomuceno, & Mendenhall, 2011).

Furthermore, testosterone has been described as a "social hormone" and is often related to behaviors such as status seeking and social dominance (Eisenegger, Haushofer, & Fehr, 2011). Single time-point measurements of testosterone correlate positively with high dominance in both adolescents (Rowe, Maughan, Worthman, Costello, & Angold, 2004; Vermeersch, T'Sjoen, Kaufman, Vincke, & Van Houtte, 2010) and adults (Carré, Putnam, & McCormick, 2009; Grant & France, 2001; van den Bos, Golka, Effelsberg, & McClure, 2013). However, according to Wingfield's challenge hypothesis, testosterone predicts social behavior only when status is threatened or challenged (Josephs, Newman, Brown, & Beer, 2003; Wingfield, Ball, Dufty, Hegner & Ramenofsky, 2013). For instance, a review by Sapolsky (1991) showed that testosterone predicts social rank in primates only when hierarchy in the group is unstable. Consequently, the effects of testosterone on behavior are highly context dependent. There is an interesting parallel here with behavioral studies on risk taking and impulsive behavior, which have found adolescents to show more risky behavior in arousing and social contexts. These findings may in turn be related to the context-specific effects of testosterone. Whatever form the underlying relationships prove to take, it is clear that the context needs to be taken into account when considering effects of pubertal hormones on adolescent behavior.

In sum, risky and impulsive behavior in adolescence may be attributed to (1) developmental change in motivational processing, with risky behavior increasing specifically in *arousing* contexts; (2) rapid change in gonadal hormone levels at pubertal onset. Importantly, these findings suggest a link between changes in motivational processing and changes in pubertal hormone levels. However, the mechanisms behind these effects remain unclear. Neuroscience can be a helpful tool in identifying these mechanisms.

THE NEUROBIOLOGY OF MOTIVATED ADOLESCENT BEHAVIOR

Over the past decades, numerous studies have investigated adolescent brain development (for a review, see Crone & Dahl, 2012), and several closely related theoretical models have emerged. The most influential are the dual-system models (Casey, Getz, & Galvan, 2008; Steinberg, 2008) based on the two-system model of willpower by Metcalfe and Mischel (1999), which postulates a cool, cognitive "know" system and a hot, emotional "go" system. The cool system enables self-regulation and self-control by being cognitive, emotionally neutral, flexible, slow, and strategic. The hot system is the origin of emotionality, fears and passion, and is driven by impulsive and reflexive forces. These two systems are in continuous interaction; their balance varies as a function of stress, developmental level, and individual self-control. Neural dual-system models propose that increased risk taking in adolescence is the result of an interaction between distinct brain networks: a motivational system associated within subcortical limbic structures, including the striatum, and a control system associated with the prefrontal cortex.

The triadic model by Ernst et al. (2014) further distinguishes between approach and avoidance behavior. In this model, the limbic system is divided into two subsystems: the ventral striatum, which is particularly sensitive to rewards and is thus associated with approach, and the amygdala, which is particularly responsive to aversive or fearful stimuli and is thus associated with avoidance.

Importantly, neurodevelopmental models suggest that changes in adolescent behavior are specifically due to the differential developmental patterns of these distinct systems. Moreover, all models emphasize the special role of the motivational system in early adolescence. Specifically, it is hypothesized that a rapid increase in dopaminergic activity within the motivational system leads to increased reward seeking during early adolescence. At the same time, the slower maturation of cognitive control systems results in unregulated or risky behavior, "like driving a car with a sensitive gas pedal and bad brakes" (Steinberg, 2014). Consequently, unregulated reward seeking may result in heightened vulnerability to risk taking during adolescence.

Although all models predict that the motivational brain system develops early in adolescence, evidence has been mixed. In line with the models' predictions, some studies have found that the ventral striatum, an important region in the brain's reward circuitry, shows peak activity in adolescence (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Galvan et al., 2006); others have found no such evidence (e.g., Bjork, 2004; Bjork, Smith, Chen, & Hommer, 2010; Richards, Plate, & Ernst, 2013). Richards et al. (2013) systematically reviewed the fMRI reward paradigms used in studies with adolescents versus adults and found task design to have a sizable impact as one source of variability across findings. However, they highlighted that the mixed results cannot be attributed solely to the type of task and that it remains unclear how other variables, such as pubertal status and environmental context, influence the neural systems underlying reward-related behavior.

One possible reason for the mixed findings is that most studies focused on age rather than using direct measures of pubertal status. Yet chronological age is not a reliable predictor of pubertal status. For instance, data from a five-year longitudinal study in the 1970s showed that puberty may begin from age 8.0 to 14.9 years in females and from age 9.7 to 14.1 years in males and is complete by age 12.4 to 16.8 years in females and by age 13.7 to 17.9 years in males (Lee, 1980). Given the considerable degree of individual difference in pubertal onset, it seems likely that many studies with a focus on chronological age have failed to detect pubertal changes in motivational behavior and related brain activity.

Indeed, a handful of studies suggest that pubertal status is a good predictor of reward-related activity. For example, a recent longitudinal study by Braams et al. (2015), using a large sample ($N = 299$), found that the average developmental trajectory of nucleus accumbens (NAcc) activation, an important region in the brain's reward circuitry (see Fig. 1), showed an inverted U-shape pattern. Moreover, change in NAcc activation was positively correlated with change in pubertal testosterone. This finding is in line with previous research reporting a relationship between pubertal testosterone and ventral striatum activity (Forbes et al., 2010; Op De Macks et al., 2011). For instance, Forbes et al. (2010) found that testosterone was positively associated with striatal activity during reward anticipation in boys, but negatively correlated with outcome-related caudate reactivity. Their finding suggests that the effects of testosterone on reward processing may be variable and depend on the decision phase.

What is still missing is a clear understanding of how hormones may lead to changes in striatal activation. Animal studies may be informative here, as puberty is not specific to humans but is a cross-species phenomenon (Spear, 2004). Indeed, single-unit recordings and lesion studies in animals have provided numerous insights into the mechanisms that underlie brain and behavioral changes during adolescence (Spear, 2004; for a review, see Casey, Duhoux, & Cohen, 2010). For instance, it is well established that dopamine plays an important role in goal-directed behavior, reward, and motivation (see Schultz, 2015). There are two major pathways of dopamine projection (see Fig. 1). First, the meso-corticolimbic dopamine system is associated with reward, learning, and motivation. Central regions of this system include the ventral tegmental area (VTA), the NAcc, and the prefrontal cortex. Second, the nigrostriatal dopamine system (Ilango et al., 2014; Rossi, Sukharnikova, Hayrapetyan, Yang, & Yin, 2013), which was originally associated with motor function (Wise, 2004), originates in the substantia nigra, where dopamine neurons primarily project to the dorsal striatum.

Animal studies have found evidence of adolescence-specific changes in both dopamine pathways. Focusing on the nigrostriatal pathway in periadolescent rodents, for instance, Stamford (1989) found reduced basal dopamine levels in adolescence. Laviola, Macrì, Morley-Fletcher, and Adriani (2003) interpreted these findings as a reason for lower basal levels of motivation and general underarousal, possibly resulting in typical human adolescent characteristics such as boredom and dissatisfaction. Interestingly, general underarousal is thought to lead to sensation seeking (Herpertz & Sass, 2000). Note, however, that adolescent rodents do not generally have less dopamine per se than adults; in fact, they have a larger dopamine storage pool (Stamford, 1989). In rewarding contexts, such as novel environments that can be explored, dopamine release is higher in adolescent than in adult rodents (Laviola, Pascucci, & Pieretti, 2001). Consequently, the potential amount of dopamine release is higher in adolescence than in adulthood, but this potential can be reached only when a stimulating context is given.

Sex steroids are known to modulate dopamine signaling and may thus play an important role in regulating adolescent developmental changes in the dopamine system (Sinclair, Purves-Tyson, Allen, & Weickert, 2014). For instance, several studies with adolescent rodents have indicated a regulating effect of testosterone on dopamine neurotransmission. Purves-Tyson et al. (2012) investigated whether gonadectomy (the surgical removal of testes or ovaries) or experimental augmentation of testosterone influences dopamine levels. On the one hand, they found testosterone to be positively associated with increases in enzymes that play an important role in dopamine metabolism (e.g., catechol-*O*-methyltransferase [COMT], monoamine oxidase A [MAOA], and monoamine oxidase B [MAOB]). Specifically, these enzymes break down dopamine into its essential parts and are involved in its inactivation. Testosterone may thus lead to inactivation of dopamine. On the other hand, Purves-Tyson et al. (2012) also found testosterone to be associated with increases in the enzyme tyrosine hydroxylase (TH), which is an integral part of the dopamine synthesis process. Thus, testosterone may increase local dopamine production in the substantia nigra. Taken together, these results suggest that testosterone has multifaceted effects on dopamine functioning, with various behavioral consequences. Specifically, the findings are in line with the idea that adolescents generally feel underaroused due to lower dopamine levels (Laviola et al., 2003). However, when they find themselves in novel, rewarding environments, more dopamine may be released from their larger storage pool, making them more risk taking and impulsive.

In a second study, Purves-Tyson et al. (2014) looked at the proteins responsible for dopamine packaging and reuptake (e.g., vesicular monoamine transporter [VMAT] and dopamine transporter [DAT]), as well as dopamine receptors (DRD1–D5) and investigated whether they were changed by testosterone in the nigrostriatal pathway of adolescent male rats. Their results suggested that increased testosterone at adolescence may change the dopamine responsivity of the nigrostriatal pathway by modulating the capacity of neurons to transport and respond to dopamine. For instance, pubertal testosterone led to an increase in excitatory dopamine receptors in the substantia nigra and the striatum, possibly reflecting greater sensitivity to dopamine via testosterone exposure. Furthermore, the general increase in dopamine receptors in the substantia nigra in response to adolescent testosterone may mirror changes in the available dopamine. Consequently, testosterone may lead to more midbrain dopamine signaling during puberty, presumably modulating reward-related decision making, such as risk taking and impulsive behavior in adolescence.

Interestingly, Purves-Tyson et al. (2014) also found differential effects of testosterone on dopamine transportation and synthesis in the substantia nigra versus the dorsal striatum: Whereas dopamine activity in the dorsal striatum was increased after gonadectomy and weakened by testosterone replacement, the opposite was true in the substantia nigra. Consequently, these results suggest that the regulation of dopamine-related molecular parameters by testosterone is greater in the substantia nigra than in the dorsal striatum. This interpretation is in line with the findings of a study by Matthews, Bondi, Torres, and Moghaddam (2013) showing that early-adolescent male rats have decreased dopamine release and synthesis in the dorsal striatum.

In conclusion, studies in adolescent male rodents have shown that testosterone has differential effects across dopaminergic pathways, increasing dopamine neurotransmission in the substantia nigra and decreasing dopamine levels in the dorsal striatum. In order to disentangle the site-specific effects of testosterone, it is crucial to investigate the functional outcomes of these molecular changes. Specifically, researchers need to understand the context dependency of the effect of testosterone, which may be due to interactions with other neuromodulators and/or hormones. Another question to be addressed is how developmental changes on a molecular level are related to brain activity as measured by the blood-oxygen-level dependent (BOLD) signal. Studies with adolescent male rats give reason to believe that testosterone impacts the motivational system. However, this interaction is likely to be complex and many unknowns remain, including how testosterone-induced molecular changes in the VTA, the substantia nigra, and the dorsal and ventral striatum influence behavior.

IMPLICATIONS

The risk taking behavior typical of adolescence results from an interaction of biological and environmental influences. As noted throughout this chapter, adolescents show unique developmental brain characteristics that are associated with particular behavioral patterns. Clearly, the best way to reduce maladaptive behavior in teenagers is not to try to change their nature by teaching them to think differently. Telling teenagers about the risks of smoking marijuana and drunk driving or instructing them to consider the potential consequences of their actions is unlikely to change their behavior (Albert & Steinberg, 2011). Instead, the focus should be on the surrounding context and on ensuring that it matches teenagers' biological developmental state and capabilities.

For instance, pubertal hormones have shown to influence the circadian rhythm, leading the typical 12-year-old to stay up later and sleep in later on weekends. In combination with the use of devices like TV or computers, this small biological change can result in sleep deprivation, which can in turn lead to behavioral problems. Specifically, the blue light spectrum has strong effects on the human circadian system, leading to late and restless sleep (see Peper & Dahl, 2013). Limiting teenagers' access to devices absorbing blue light at night may reduce the risk of pubertal effects on the circadian system resulting in health problems such as sleep deprivation. Another idea would be to delay the start of the school day to 10 am, thus ensuring that teenagers get enough sleep.

More generally, policy and regulations need to be modified to limit teenagers' opportunities to engage in risky behaviors. Steinberg (2015) offers concrete policy recommendations that focus primarily on restricting the time that adolescents are left unsupervised.

SUMMARY AND FUTURE DIRECTIONS

In this chapter, we have sought to integrate findings elucidating the specific impact of pubertal hormones on motivational processes in adolescence. A rapid change in gonadal hormone levels at pubertal onset has been linked to motivational changes that may prompt increased risk taking and impulsivity during adolescence. Mechanisms that mediate this relationship are associated with a neuronal motivation system, in which dopamine is of special interest. Neurobiological models of adolescent brain development highlight the impact of pubertal hormones on reward-related regions, resulting in strong reward-approach behavior, which is in turn hypothesized to account for increased risk taking and impulsivity in adolescence. Although the current literature does not offer unreserved support for the hypothesis that reward-sensitive brain regions are more responsive during adolescence, rodent studies have highlighted the impact of testosterone on dopamine neurotransmission in the substantia nigra. However, there is a lack of research that specifically (1) tests the relationship between pubertal hormone levels and risky and impulsive behavior in adolescence; (2) investigates the impact of pubertal hormone levels on brain regions associated with motivational processing; (3) describes how the relationship between pubertal hormones levels and brain regions changes over time; and (4) explains how this change is linked to developmental changes in risk taking and impulsivity.

To address these questions, we propose the following directions for future research into pubertal effects on behavior and brain functioning: First, studies should apply measures of pubertal age, ideally hormonal, as well as assessing chronological age. Second, the integration of different levels of analysis is essential. Studies that combine measures of behavior, its neural correlates, and how they interact with pubertal hormones such as testosterone in specific contexts are needed. Third, and most importantly, assessments at multiple time points are needed to capture intraindividual change over time. Longitudinal studies of development are imperative and can provide insights into interactions early versus late in puberty. Finally, gender differences must be considered, and hormones other than testosterone that undergo rapid changes during adolescence should also be investigated (e.g., estradiol and oxytocin).

In summary, investigating developmental changes on a hormonal level and focusing on neurotransmitters such as dopamine in the human adolescent brain is a promising avenue for gaining further insights into the specific neurobiological mechanisms underlying risky and impulsive behavior in adolescence.

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CHILDREN'S INHIBITORY CONTROL WHEN FACING NEGATIVE EMOTIONS

Tali Farbiash and Andrea Berger

ABSTRACT

Inhibitory control (IC) is a central executive function that shows significant development throughout the preschool years. IC is known as a factor that underlies the ability to self-regulate in daily situations. This ability is challenged when a child faces negative emotions; a challenge that is seen in children's IC performance and brain activity. This chapter elaborates on the effects that negative emotional experiences have on children's IC functioning. Moreover, previous studies regarding the way emotional experiences are reflected in brain activity are included. Additionally, this chapter will offer a comprehensive review of the factors affecting individual differences in IC, including the role of children's temperamental effortful control and negative affectivity. Further, the role of parenting behaviors will be discussed, focusing on the way in which maternal self-regulation influences child inhibitory control, including related educational implications.

Keywords: Inhibitory control; negative affectivity; event-related potentials; N2; theta frequency; kindergartners

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INHIBITORY CONTROL

Inhibitory control (IC) is an executive function defined as the ability to deliberately suppress dominant, automatic, or prepotent responses (Rothbart, Ahadi, Hershey, & Fisher, 2001). It implies the ability to exert top-down control and act voluntarily according to the requirements of a situation. Without IC, our behavior would be involuntarily driven by impulses and habits and/or from the characteristics of the environmental situation (Diamond, 2013).

IC undergoes significant development during the preschool years (Carlson, 2005; Kochanska, Coy, & Murray, 2001; Kochanska, Murray, & Harlan, 2000; Zelazo, Müller, Frye, & Marcovitch, 2003). The ability to inhibit inappropriate responses is required by young children in many daily situations, for example, when they are asked to wait their turn, to stop an enjoyable activity when needed, to listen to a story while inhibiting other temptations, and so forth. Accordingly, children's ability to inhibit inappropriate responses and self-regulate at the preschool age is associated with their ability to internalize rules and follow directions (Eisenberg et al., 2004, 2005; Rhoades, Greenberg, & Domitrovich, 2009). It is also associated with their subsequent social-emotional capacity and adaptive functioning (see reviews in Berger, 2011; Calkins & Marcovitch, 2010; Eisenberg et al., 2004), academic achievements (e.g., Denham, Warren-Khot, Bassett, Wyatt, & Perna, 2012), and even their physical health and criminal behavior in adulthood (Moffitt et al., 2011).

In terms of brain function, IC abilities are considered to be related to activity in the prefrontal and dorsolateral cortices regions (Casey et al., 1997; Durston et al., 2002; Lamm & Lewis, 2010; Marsh et al., 2006). Furthermore, the process of over-riding a prepotent response usually elicits conflict between incompatible responses (Braver, Barch, Gray, Molfese, & Snyder, 2001), which is often evident in the activity of the anterior cingulate cortex (ACC; Botvinick, Cohen, & Carter, 2004; Braver et al., 2001; Rueda, Posner, & Rothbart, 2005). The development of IC occurs in parallel to the maturation and connectivity of the prefrontal cortex (PFC; Berger, 2011; Posner & Rothbart, 2000; Wolfe & Bell, 2007). This maturational process is seen with neuronal proliferation and pruning, which begins in pregnancy and continues throughout infancy, childhood, and even adolescence. Moreover, progressive thinning of gray matter, which is associated with the myelination process, is concurrent with brain growth during childhood (for a detailed review see Berger, Kofman, Livneh, & Henik, 2007). Throughout the preschool years, IC development is reflected in a child's transition from infantile behavior – which lacks self-regulation and leans on the caregiver for soothing and regulation – toward greater maturity and an increasing ability to self-regulate. Indeed, in research studying this ability, IC increased with age, as demonstrated in the performance of various inhibitory tasks (Carlson, 2005; Kochanska et al., 2000, 2001; Zelazo et al., 2003).

Competition between two or more incompatible responses often occurs in the kindergarten years, when children are asked to do *x*, when they actually want to do *y*. Such a conflictual situation is emotionally aversive for many children, probably because of the anticipation of negative consequences that may accompany a failure to resolve the conflict (Leue, Lange, & Beauducel, 2012). In this case, the negative emotional experience can challenge the child's ability to inhibit the inappropriate, dominant behavior and instead perform a subdominant, although more appropriate, behavior. Thus, it appears that a child's ability to regulate his/her emotional experience is crucial for IC.

IC AND NEGATIVE EMOTIONS

Experiencing negative emotions can influence a subject's IC performance; however, there are contradicting results in the extant literature regarding the direction of this effect (Cohen & Henik, 2012; Eysenck, Derakshan, Santos, & Calvo, 2007; Mitchell & Phillips, 2007; Pessoa, Padmala, Kenzer, & Bauer, 2012). Several studies have shown that negative emotions can impair executive performance (Cohen-Gilbert & Thomas, 2013; Padmala, Bauer, & Pessoa, 2011; Verbruggen & De Houwer, 2007) and that emotional content can receive prioritized attention (Pessoa, 2009). Thus, it seems, the process of emotion regulation consumes the available attentional resources needed for cognitive functioning and the executive, inhibitory functions are impaired (Cohen & Henik, 2012). However, other studies have shown that negative emotions can result in improved executive performance (Chajut & Algom, 2003; van Steenbergen, Band, & Hommel, 2011). One of the explanations offered for this improvement is that the negative emotional experience evoked children's more focused, goal-oriented attention to minimize their negative emotional experience (Cohen & Henik, 2012). Such an attentional narrowing was evident in previous studies, which showed that stress/threat improved selective attention (Chajut & Algom, 2003; van Steenbergen et al., 2011). Furthermore, improvement in

IC performance may also be related to the relevance of the negative emotional experience to the task (Kanske, 2012; Kanske & Kotz, 2011). Thus, it may be that a child's negative emotional experience signals a problematic situation that requires the recruitment of more efficient and/or more attentional resources, resulting in accelerated task performance. It may also be that a child's IC performance will not be harmed; however, children will need to exert enormous effort to both recruit the attentional resources for exerting IC *and* to regulate the negative emotional experience (Eysenck et al., 2007). In this case, IC performance will not be negatively affected, but an emotional price will be probably paid (Farbiash, Taase, Meiri, Faroy, & Berger, in preparation).

Previous literature has described the close link between motivation and emotion (Pessoa, 2009), thus several studies have used motivational manipulations to elicit an emotional experience. For example, it has been shown that penalties, such as losing points in a game, strongly evoke a child's negative emotional experience which, in turn, increases the need for emotion regulation (Farbiash & Berger, 2015; Lamm & Lewis, 2010; Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006). The results regarding the effect of a negative emotional experience on children's response inhibition are inconsistent. Lewis et al. (2006) and Lamm and Lewis (2010) investigated elementary-school children and found that children who experienced higher levels of frustration (as a result of the "losing point" condition) also exhibited lower IC performance. In contrast, Farbiash and Berger (2015), who investigated kindergartners, found the opposite effect: Children's performance was better when more negative emotions were reported, meaning, in the "losing point" condition compared to the "winning" condition. It should be noted that these studies did not intend to investigate the separate effects of motivational versus emotional aspects on children's IC performance, but rather, were intended to examine the effect of the need for emotional regulation in addition to the inhibition of a response.

IC, NEGATIVE EMOTIONS, AND CORTICAL BRAIN ACTIVITY

The brain processes that are active when children are required to exert IC are often investigated using the electrophysiological measures of event-related potentials (ERP). To collect ERP data, researchers use the encephalogram (EEG). This method has the advantage of high temporal resolution, which can capture rapid changes in neural processing and also detect subtle processes that are not expressed in overt behavior (Dennis, 2010).

ERP waveforms are typically described in terms of positive and negative peaks, which are labeled as ERP components (measured in μV). One of the most frequently studied ERP components – in relation to IC performance and conflict monitoring – is the N2 and its amplitude (e.g., Donkers & van Boxtel, 2004; Lewis et al., 2006; Nieuwenhuis, Yeung, van Den Wildenberg, & Ridderinkhof, 2003). The N2 (sometimes also called the N200) is the second negative peak in a waveform, recorded approximately 200–400 ms following the stimulus; it usually appears at the electrodes located in the fronto-central areas of the scalp (Falkenstein, Hoormann, & Hohnsbein, 1999; Jodo & Kayama, 1992). The "N" stands for negative and the "200" stands for 200 ms. Because the brain activity shows oscillations at a variety of frequencies, it is important to measure not just the amplitude (the amplitude size in this case) as an index of brain activity, but also the power of the frequencies embedded in this amplitude. This means that each amplitude contains a range of frequencies and that each frequency has a different strength (i.e., the power) for a specific point in time. Time-frequency (T-F) analyses using wavelets allow for the examination of the power of a specific frequency, measured in $(\mu V)^2$ (Samar, 1999). At the frequency level, theta EEG signals (4–8 Hz) are related to response inhibition (Liu, Woltering, & Lewis, 2014; Nigbur, Ivanova, & Stürmer, 2011), to conflict detection (Tzur & Berger, 2007), and to conflict monitoring (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). T-F analyses also show that the theta oscillations are reflected in the N2 component (Balconi & Pozzoli, 2009; Harper, Malone, & Bernat, 2013) and that the ACC brain area is the main common generator of both N2 (Nieuwenhuis et al., 2003) and theta EEG signals (Harper et al., 2013).

One of the neuropsychological tasks designed to investigate response inhibition while measuring brain activity is the Go/NoGo task. In standard Go/NoGo paradigms, participants are required to press a button as fast as possible for a particular category of stimuli (Go trials) and to withhold or suppress a response for another category of stimuli (NoGo trials; Garavan, Ross, & Stein, 1999). Previous ERP studies using the Go/NoGo task showed larger N2 amplitudes in successful NoGo trials compared to Go trials with adult participants (Falkenstein et al., 1999; Jodo & Kayama, 1992; Kirmizi-Alsan et al., 2006; Lavric, Pizzagalli, & Forstmeier, 2004) and with children (Johnstone, Pleffer, Barry, Clarke, & Smith, 2005; Todd, Lewis, Meusel, & Zelazo, 2008). Fig. 1 presents a typical example of the N2 amplitude during a Go/NoGo task. Of importance to the interpretation of

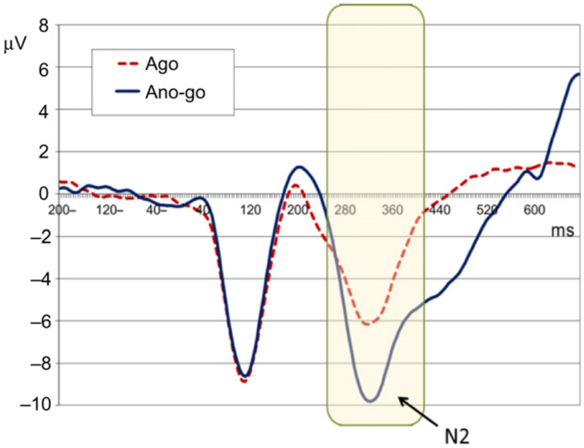

Fig. 1. This Graph Presents Children's N2 Amplitudes during a Go/NoGo Task.

Fig. 1: The NoGo (solid) line associated with response suppression shows a stronger response (−10 μV) than the Go (dotted) line associated with response release (−6 μV) during the N2 time interval.

A recent study investigating conflict monitoring in preschool and school-aged children showed that N2 amplitudes are larger during conflict monitoring, but only for the children in the older age group (Buss, Dennis, Brooker, & Sippel, 2011). As for the emotional experience, findings show that response inhibition evoked larger N2 amplitudes during a negative emotion condition compared to a nonemotion condition (Lamm, White, McDermott, & Fox, 2012; Lewis et al., 2006; Yuan et al., 2011). Furthermore, children's reports of their negative emotional experience have been associated with larger inhibitory N2 amplitudes during an emotion-induction manipulation (Lewis et al., 2006). The larger N2 amplitudes were interpreted to be a reflection of higher effortful activation of the inhibitory brain mechanisms required when feeling emotionally distressed (Lewis & Stieben, 2004).

Studies investigating IC performance with a T-F approach have been conducted mostly in adults. Results from these studies indicate larger theta power during successful inhibition of NoGo trials compared to Go trials of the Go/NoGo task (Harper et al., 2013; Kirmizi-Alsan et al., 2006; Nigbur et al., 2011) and larger theta phase synchrony – which also indicates higher theta power – during conflict processing (Nigbur et al., 2012). Theta oscillations are also seen in relation to emotional arousal and emotional regulation (Balconi & Pozzoli, 2009; Knyazev, 2007; Rodríguez, Rey, Clemente, Wrzesien, & Alcañiz, 2015). For instance, Ertl, Hildebrandt, Ourina, Leicht, and Mulert (2013) found that theta power was larger during a demand for regulating negative emotions.

Studies that have conducted T-F analyses to explore emotional effects on children's brain activity are limited, although they support the notion of larger theta power during emotional circumstances. For instance, Farbiash and Berger (2015) have shown that children's theta power increased when they experienced negative emotions resulting from a motivational manipulation, specifically, when children lost points in a game, compared to when they gained points. It seems that the negative emotional experience enhanced children's conflict between inhibiting and releasing prepotent responses, which was reflected in the increased difference between theta power in the response inhibition condition compared to the response release conditions (see Fig. 2). Liu et al. (2014) investigated theta activity during response control in children and adolescents and found that – only in adolescents – theta power increased when participants needed to exert effort to regain their points and avoid losing in a game. Cavanagh and

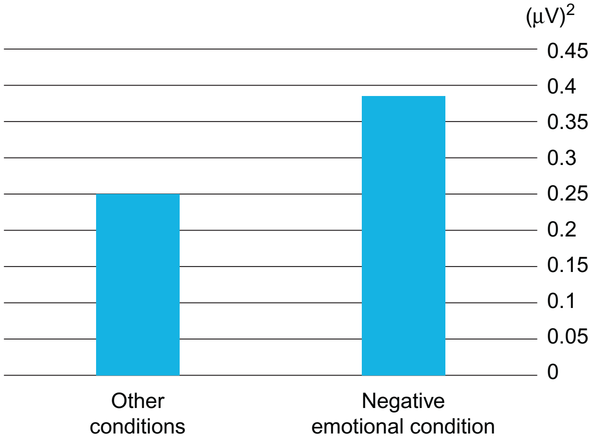

Fig. 2. Theta Power Differences between Response Inhibition (NoGo Trials) and Response Release (Go Trials) in the Negative Emotional Condition (where Children Lost Points during a Game) Compared to the Other Conditions (where Children Gained Points during a Game). A larger magnitude indicates that the theta power was more salient at that specific moment in time when the child's EEG was recorded.

Shackman (2015) suggested that negative emotions, such as fear and anxiety, are expressed with larger frontal midline theta oscillations and are associated with a more cautious or inhibited response, which is made in the face of an uncertainty, such as when an aversive outcome is possible.

IC, NEGATIVE EMOTIONS, AND TEMPERAMENTAL INDIVIDUAL DIFFERENCES

As detailed thus far, motivational manipulation, accompanied with negative emotional experience, influences an individual's ability to inhibit responses when required, although the extant literature is not clear regarding the exact direction of this effect. Moreover, it is apparent that a negative emotional experience is related to increased brain activity, as expressed by larger N2 amplitudes and increased theta power seen in the prefrontal areas of the cortex.

Taking an *individual differences* approach allows an investigation of these influences and associations, beyond the group level, considering that negative emotional experiences affect different children in a different way. In other words, when looking at the differences between children's performance during distress, it appears that although some of the children perform better under stressful conditions, others actually perform worse. What characterizes children who manage to cope with and channel the negative emotional experience into a better performance? Further, what characterizes children who succumb to the negative emotional experience and have a decline in their performance as a result? The source for these marked individual differences could rely partly on the constitutional and biologically rooted core characteristics of the children, which can be defined as *temperament*.

Temperament refers to individual differences in reactivity and self-regulation (Cole, Martin, & Dennis, 2004; Rothbart, 1989, 2011; Rothbart & Rueda, 2005). Reactivity accounts for the extent to which a subject's motor, affective, and sensory response systems are aroused, whereas self-regulation accounts for the processes that serve to modulate (increase or decrease) this reactivity (Rothbart et al., 2001). The emotional reactive tendency to experience negative emotions, distress, and frustration (including its latency, intensity, and duration) is known as negative affectivity (NA). Positive affectivity is also a reactive tendency; however, it is not included in the focus of this chapter. Effortful control (EC) includes the attentional capacities that serve to self-regulate the emotional experience, including attentional focusing and shifting, the ability to perform actions that are usually avoided, as well as the ability to inhibit prepotent responses, which is also known as IC (Rothbart, Ahadi, & Evans, 2000; Rothbart et al., 2001; Rothbart & Rueda, 2005). Developmentally, emotional reactivity begins to emerge in the early months of life. In contrast, regulatory effortful mechanisms develop later on, around the preschool and kindergarten years (Berger, 2011; Rothbart & Rueda, 2005; Rothbart et al., 2000). Although EC is not developed at birth, it is genetically based (Fan, Wu, Fossella, & Posner, 2001; Fossella et al., 2002; Rothbart & Posner, 2005; Rothbart, Sheese, & Posner, 2007).

Temperamental individual differences in children's EC and NA are relatively stable characteristics (Eisenberg et al., 2005; Kochanska & Knaack, 2003; Kochanska et al., 2000; Rothbart, 2011; Rothbart et al., 2000) and are associated with a wide array of developmental outcomes, both concurrently and overtime. For instance, children's EC has been concurrently correlated with externalizing and internalizing problems (Eisenberg et al., 2004) as well as with children's social functioning (Liew, Eisenberg, & Reiser, 2004; Spinrad et al., 2006), academic functioning (Neuenschwander, Röthlisberger, Cimeli, & Roebers, 2012), and theory of mind (Carlson & Moses, 2001). Concurrent correlations have also been found between children's negative emotionality and their social development (Kochanska et al., 2000; Liew et al., 2004). Studies have also shown that externalizing problems later in life are predicted by EC (Eisenberg et al., 2004; Spinrad et al., 2006) and negative emotionality (Eisenberg et al., 2004). Additionally, negative emotionality predicts children's social competence (Sallquist et al., 2009). The associations between temperament and children's developmental outcomes are seen separately for EC and NA; however, these two mechanisms coexist and may interact with each other to influence children's adjustment (Lengua, 2003). For instance, the combined effect of high levels of NA and low EC were associated with higher levels of behavioral problems, whereas low levels of NA and high levels of EC were associated with adaptive social functioning (Eisenberg, Fabes, Guthrie, & Reiser, 2000).

Given such concurrent and long-term significance of early emerging temperamental characteristics in EC and NA, extensive research has been devoted to understanding their underpinnings and correlates. Studies regarding the links between reported and/or observed EC and children's actual performance in tasks requiring IC reveal consistent – although moderate – correlations; the direction of the association suggests that higher levels of EC are related to better performance in inhibitory tasks (Wolfe & Bell, 2004) as well as in conflict tasks (Gerardi-Caulton, 2000; González, Fuentes, Carranza, & Estévez, 2001; Rothbart, Ellis, Rosario Rueda, & Posner, 2003; Simonds, Kieras, Rueda, & Rothbart, 2007). Moreover, Morasch and Bell (2011) have shown that mothers' reports of children's temperamental IC are associated with their child's performance in a conflict task as well as in an IC compliance task. As for NA, the behavioral findings show that higher levels of NA (i.e., anger, frustration, and discomfort) are associated with lower IC (Calkins, Dedmon, Gill, Lomax, & Johnson, 2002; Kochanska & Knaack, 2003; Wolfe & Bell, 2004) and greater interference in conflict tasks (González et al., 2001; Rothbart et al., 2003).

How are the combined temperamental characteristics in EC and NA responsible for individual differences in IC? EC and NA are known to be inversely related (Eisenberg et al., 2005; Rothbart & Rueda, 2005). Thus, it is reasonable to expect that high EC and low NA would be associated with higher performance in executive (including IC) tasks. Additionally, the effect that negative emotions have on executive performance could be modulated by factors such as the subject's ability to exert top-down control and to regulate the negative emotional experience (Cohen & Henik, 2012). It is well established that the cognitive, attentional capacities embedded in the notion of EC serve to modulate emotions (Ochsner & Gross, 2005; Rueda et al., 2005; Rueda, Posner, & Rothbart, 2004; Sheppes & Levin, 2013; Sheppes et al., 2012). Moreover, since attentional resources are limited and negative emotions usually capture attention (Mitchell & Phillips, 2007; Pessoa, 2009), it is reasonable to assume that subjects with better attentional abilities will also be able to inhibit responses while regulating a negative emotional experience.

Children high in negative emotionality are also expected to experience high levels of arousal when confronted with stressful or threatening situations (Donzella, Gunnar, Krueger, & Alwin, 2000; Rueda & Rothbart, 2009). Studies that are derived mostly from adult populations have shown that anxious individuals are distinctively sensitive to threatening stimuli and thus show attentional bias to this threat-related stimuli (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007; Mathews & MacLeod, 2002); however, these studies did not refer to the emotional experience these individuals actually experience during exposure to the threatening stimuli. Individual differences in NA and the effects that a negative emotional experience may have on performance during an inhibitory task have not been extensively investigated in children. Eysenck et al. (2007)

have discussed the effects of individual differences of negative affect (e.g., anxiety and worry) on adult IC. They suggest that anxious individuals are less efficient, meaning they invest more effort or resources to achieve the same results that nonanxious individuals do. According to Eysenck et al. (2007), individuals with a higher tendency to experience negative emotions are also more distracted by internal thoughts (e.g., worrying, self-preoccupation) as well as by external stimuli. Thus, their performance on an inhibitory emotional task may be less efficient and even less effective. Because emotion and cognition interact, it is suggested that the efficiency of the cognitive, EC of emotions will also depend on the intensity of the emotional experience (Pessoa, 2009; Rueda et al., 2005).

EC AND NA AS REFLECTED IN BRAIN ACTIVITY

Temperamental individual differences in EC and NA and their expression in the children's IC task have been extensively studied using behavioral approaches. However, the way these individual differences are reflected in children's brain activity is less understood. As for EC and the N2 amplitude, previous studies reveal quite inconsistent results: On the one hand, studies indicate that individuals high in EC seem to need less recruitment of neural resources when resolving conflict. For example, Buss et al. (2011) showed that lower levels of temperamental EC were correlated with larger N2 amplitudes. Additionally, they found that preschool and school-aged children who had smaller conflict interference also had smaller N2 amplitudes. These results are consistent with the findings of Dennis and Chen (2009), who showed that, in adult participants, more efficient executive attention was associated with smaller N2 amplitudes. On the other hand, there are some studies that have found that better attentional control in children is actually associated with larger N2 amplitudes (Dennis, Malone, & Chen, 2009; Pérez-Edgar & Fox, 2007). In these studies, smaller N2 amplitudes were interpreted to be reflections of less efficient IC processes.

Regarding individual differences in NA, findings are much more consistent and show that high NA (i.e., anxiety and frustration) is associated with larger N2 amplitudes in adults (Dennis & Chen, 2007, 2009) as well as in children (Hum, Manassis, & Lewis, 2012; Pérez-Edgar & Fox, 2007). Additionally, Lewis et al. (2006) showed that children who reported themselves as highly frustrated during the negative emotional induction also needed to devote more neural resources to successfully inhibit responses

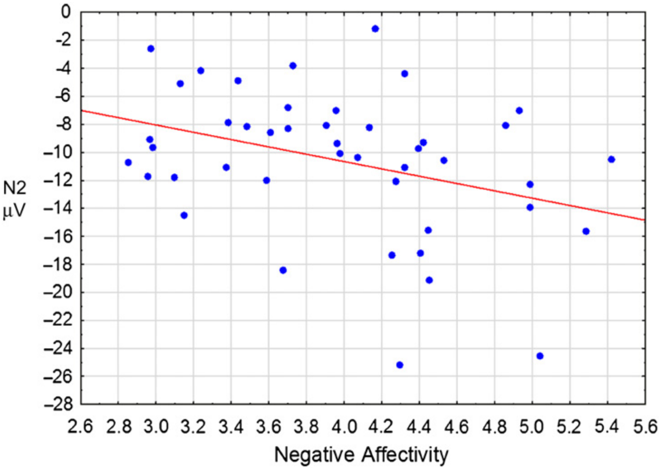

Fig. *3*. Scatterplot of the N2 Amplitudes (*x*-Axis) and Temperamental NA (*y*-Axis) during the Negative Emotional Experience.

and monitor conflicts when required. Recently, Farbiash et al. (in preparation) found that the tendency of children to experience NA as a result of a negative emotional experience was correlated with larger N2 amplitudes (see Fig. 3). Their results also show that higher levels of kindergartners' NA were associated with larger theta power differences between NoGo and Go trials, as a result of the negative emotional manipulation (see Fig. 4). The effects of kindergartners' NA were seen in Farbiash et al.'s research (in preparation) at the level of brain activity, but not in behavior. These results emphasize that emotional risk is not always behaviorally evident and that emotional and attentional efforts should also be taken in to account.

Although the Farbiash et al. study (in preparation) is innovative in its T-F analysis in young children, findings are still consistent with the previous adult studies showing that the theta power seen in the frontal and PFC is increased when facing conflict (Nigbur et al., 2012; Tzur & Berger, 2007), such as when response inhibition is required (Liu et al., 2014; Nigbur et al., 2011). It appears that for kindergartners' high in NA, the emotional manipulation is more intensely experienced, the conflict between the competing responses is enhanced, exerting emotional regulation is more difficult, and theta power seen as a result is thus larger. As for EC, preliminary results obtained from Farbiash et al. (in preparation) show that children who had better inhibitory performance during a negative

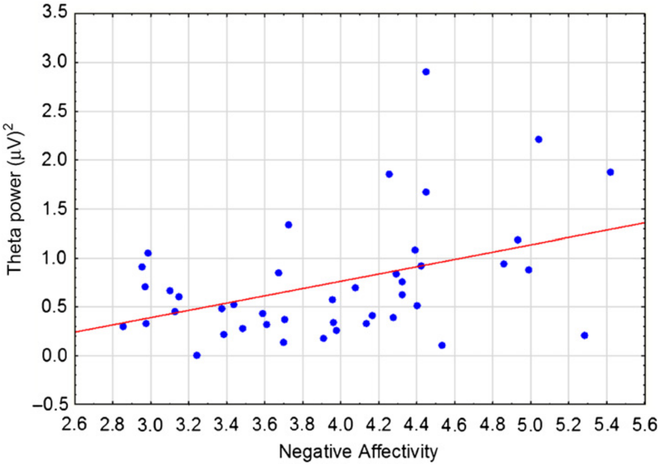

Fig. 4. Scatterplot of the Power of Theta Frequency (µV)^2 (*x*-Axis) and Temperamental NA (*y*-Axis) during the Negative Emotional Experience.

emotional experience also had less theta power in successful inhibition of NoGo trials. No significant results were found for kindergartners' EC, although this study is still ongoing.

MATERNAL SELF-REGULATION PERSPECTIVE

In addition to constitutional temperamental differences, individual differences are markedly influenced by environmental factors (Fox & Calkins, 2003). Indeed, one of the most frequently investigated environmental factors on the socialization of children's emotional regulation is parenting (Bariola, Gullone, & Hughes, 2011; Belsky, 1984; Cole, LeDonne, & Tan, 2013; Cumberland-Li, Eisenberg, Champion, Gershoff, & Fabes, 2003). Most of the literature concerning parental influences on children's self-regulation has focused on mothers. Although in recent years there has been an overall increase in fathers' involvement in raising their children, it was found that mothers still spend more time with the children and thus serve as the main caregiver (Craig, 2006; Wall & Arnold, 2007). What is the mother's role in her child's ability to inhibit responses during a negative emotional experience? It seems that mother-child relations provide many opportunities for children to train IC abilities and for mothers to respond in a way that affects children's emotional development. It has been suggested that mother-child interactions are subjected to unpleasant emotions, especially since the normal development of preschool and kindergarten children includes daily episodes of misbehavior, including noncompliance, tantrums, and so forth (Campbell, 1995; Roberts & Strayer, 1987). This misbehavior usually evokes negative maternal emotions, which affect the mother's reaction to her child (Cole et al., 2013; Dix, 1991; Lorber & Smith Slep, 2005).

One of the most prominent frameworks used to study parenting are *parenting styles*, as classified by Baumrind (1966, 1971); she indicated that different parental patterns of child rearing were associated with various developmental outcomes in children. According to Baumrind, the most effective parenting style is the *authoritative* parenting style, which is characterized by warmth as well as with the establishment of firm and consistent limits. Less effective parenting styles are the authoritarian and permissive parenting styles. Authoritarian parenting includes the use of harsh, controlling punishments, whereas permissive parenting is characterized by parents who fail to set to clear and consistent limits for their children, although their way of parenting is warm and considerate.

In accordance with these parenting styles, several studies have investigated the disciplinary behaviors that parents use and the effects of this discipline on children's self-regulation and IC performance (Colman, Hardy, Albert, Raffaelli, & Crockett, 2006; Karreman, van Tuijl, van Aken, & Deković, 2008; Lengua, Honorado, & Bush, 2007; Moilanen, Shaw, Dishion, Gardner, & Wilson, 2010; Spinrad, Stifter, Donelan-McCall, & Turner, 2004; Verhoeven, Junger, van Aken, Deković, & van Aken, 2007). For instance, the authoritative parenting style is characterized by parental responsiveness, warmth, and acceptance while accompanied by limit setting, structured daily routines, and behavioral guidance. Such a parental approach is consistently associated with a child's higher level of EC (Karreman et al., 2008; Kochanska et al., 2000). It has been suggested that parents who adopt an authoritative approach are more sensitive to their children's emotional states and, hence, their responses promote down-regulation of their children's negative emotional experiences. Additionally, responsive and sensitive reactions to children's negative feelings prevent children from experiencing extreme levels of emotional arousal, in a way that helps them learn ways to cope and control their emotional experience before it gets out of control. Authoritative parents also provide developmentally appropriate limit setting, which enables children to train their self-regulation abilities when inhibition of response is necessary (Moilanen et al., 2010).

In contrast, the authoritarian style is characterized by an over-reactive parenting strategy that results in emotional, harsh discipline, expressed with the use of negative verbal comments, negative tone, and physical behaviors (Moilanen et al., 2010; Rhoades & O'Leary, 2007). Such harsh maternal discipline has been associated with low levels of IC in children (Moilanen et al., 2010). Moreover, a mother's restricted use of physical punishment seems to predict higher levels of self-regulation in her child (Colman et al., 2006). Consistently, maternal and paternal harsh, negative controlling discipline strategies (e.g., physical punishment, denial of privileges) have been associated with lower levels of EC in children (Karreman et al., 2008).

On the other end of the discipline scale, a permissive parenting style is reflected in lax parenting strategies. Lax parenting refers to a parent being inconsistent and giving in to the child's demands when providing discipline. Spinrad et al. (2004) claim that when mothers capitulate to their children's requests when expressing negative emotions, children tend to use the expression of negative emotions as a strategy to get their desires, which results in under-controlled behavior. Indeed, it was found that nonlax maternal behavior, which includes maternal clarity and consistent limit setting, predicted higher levels of EC in children (Lengua et al., 2007). Additionally, Verhoeven et al. (2007) showed that lack of parental structure (which includes lax and over-reactivity discipline strategies of both mothers and fathers) is associated with lower IC in toddlers.

Parenting strategies can be interpreted in terms of a mother's ability to self-regulate. The previously cited studies did not differentiate between the discipline practices a parent actually uses and the discipline practices a parent believes s/he should be using; however, the parental discipline strategy a parent eventually uses may either derive from his/her perceptions and beliefs about the appropriate parenting practices to employ (e.g., using corporal punishment as a calculated, planned way of discipline) or may reflect a loss of control. Hence, this differentiation is important. For example, as suggested by Morris, Silk, Steinberg, Myers, and Robinson (2007), children model their parents' adaptive or maladaptive strategies for coping with negative emotions. Carlson (2009) referred to the process of parental socialization of children's emotional self-regulation saying, "It is perhaps a bit embarrassing for readers who are themselves parents to realize how unaware we are of the direct guidance we provide and, crucially, the indirect ways we transmit messages to children about self-regulation via modeling and family systems and organization" (p. 91).

When considering maternal self-regulation in parenting practices, less maternal regulation indicates that a mother reacts to her child's misbehavior more radically (either more lax or more over-reactive) than she intended to. Moreover, less maternal regulation as a response to her child's misbehavior reflects a mother's difficulty in handling her own – as well as her child's – negative emotional experience (Farbiash & Berger, in preparation). Over-reactive and/or lax reactions toward a child serve as a way to minimize this emotional negativity (Lorber & Smith Slep, 2005). There are some previous studies that have investigated parental variables that include some elements and aspects of self-regulation. For example, a recent study has shown that proactive parenting (which includes a set of techniques that parents adopt to minimize the child's misbehavior in potentially troublesome situations) is associated with children's EC (Chang, Shaw, Dishion, Gardner, & Wilson, 2014). One of the explanations offered for this finding was that parents' execution of proactive strategies (such as reframing the situation or redirecting attention) models self-regulatory processes for children, in other words, parents need to control their own impulses to perform goal-directed behavior.

Maternal self-reports of regulation correlate with children's emotional self-regulation (Cumberland-Li et al., 2003), and parental temperamental EC correlates with children's emotional self-regulation as well (Valiente, Lemery-Chalfant, & Reiser, 2007). Additionally, maternal executive functions have also been associated with children's executive functions and these associations were found to be stable at 24–48 months of age (Cuevas et al., 2013). Recently, Farbiash and Berger (in preparation) aimed to test the role of a mother's self-regulation in her parenting practices in kindergartners' IC during a negative emotional experience. Their results showed that lower maternal self-regulation, as reflected in lax maternal behavior, was associated with lower child IC during a negative emotional experience. This correlation remained significant even after controlling for the child's temperamental NA. It appears that children of mothers who did not react in accordance with their values and goals in terms of lax discipline were less able to cope with a negative emotional experience and continue to inhibit responses as required.

It is possible that children who are raised by less regulated, lax mothers also have fewer opportunities to learn emotion-regulation strategies. Those children who are not used to experiencing negative emotions in response to their desires being blocked are also not used to regulating negative emotions. A mother who uses a lax strategy to minimize her own negative emotional experience in response to her child's misbehavior models the strategy that the way to cope with negative emotional situations is to give up, to stop persisting, or to stop pursuing a desired goal. Hence, when the child needs to function in a negative emotional situation (e.g., to continue playing a game, although currently losing), s/he also gives in or gives up. It may also be that those mothers cannot bear the child's negative emotional reaction (probably because it evokes their own negative feelings, which they also find hard to regulate) and, therefore, they do whatever it takes to diminish their child's and their own emotional experience. Dix and Branca (2003) have proposed that distressed parents prefer to achieve short-term goals (such as "to stop the child's screaming") that tend to make parents' immediate circumstances easier, rather than pursuing long-term goals (such as promoting child's mature and socialized behavior), which takes time and energy. It seems that when facing their children's emotional states, those mothers have less emotional and behavioral alternatives, specifically, they are unable to maintain a demanding attitude and at the same time exhibit responsive and warm behavior. However, it appears that when mothers believe lax parenting is the appropriate way to parent, their lax strategies are not evolved from feelings of "losing control" and those mothers actually resist "giving in" to their children.

MATERNAL SELF-REGULATION AND CHILDREN'S IC AT THE ELECTROPHYSIOLOGICAL LEVEL

The kindergarten years are characterized by brain plasticity (Belsky & Pluess, 2009), which makes parent-child experiences in those years enormously important to children's brain development. Although there is a large body of literature regarding the influences of parenting on children's emotional and behavioral development, relatively little is known about how parenting styles influence children's brain functioning and development (for a detailed review, see Belsky & de Haan, 2011). Parenting behaviors are assumed to be an influential factor for children's executive and inhibitory functions; however, as Bell and Diaz (2012) have mentioned, "… not much attention has been given to the role of parenting to the development of executive functions" (p. 16).

As far as we know, Farbiash and Berger (in preparation) are the first to examine the way parental self-regulation, as demonstrated in parenting practices, is reflected in children's IC-related brain activity during a negative emotional experience. Their results show that children of mothers with lower self-regulation in lax parenting exhibited larger N2 amplitudes and theta power during a negative emotional experience. These findings were evident even beyond the child's temperamental NA (see Fig. 5). The interpretation for these results was that individuals with better IC need to recruit fewer neural resources to resolve conflicts and successfully inhibit responses when required. Children of less regulated mothers (i.e., mothers with lower executive abilities, EC, etc.) also have children with lower executive abilities (Cuevas et al., 2013), EC (Chang et al., 2014; Valiente et al., 2007), and emotional self-regulation (Cumberland-Li et al., 2003). Thus, the findings that those children also exhibited larger N2 amplitudes and larger theta power support the assumption that individuals with lower executive abilities show less efficient brain processing and thus need to exert more attentional resources and effort to successfully perform an IC task.

EDUCATIONAL IMPLICATIONS

This chapter integrates developmental and neuropsychological research regarding children's abilities to inhibit prepotent responses when facing

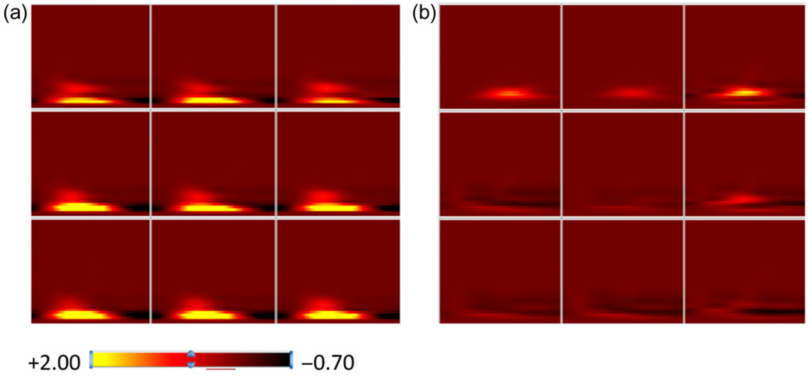

Fig. 5. The Graphs Illustrate the Power of the Theta Frequency during NoGo Trials of the Negative Emotional Condition for Two Children: The Child Whose Mother Had the Best Maternal Self-Regulation in Laxness (b) and the Child Whose Mother Had the Worst Maternal Self-Regulation in Laxness (a). *Notes*: Each panel displays the wavelet of nine middle frontal scalp electrodes that were investigated in Farbiash and Berger (in preparation). The x-axis of each panel displays time in ms and the y-axis displays frequency bands. The color palette codes for power: The brighter color reflects higher power $(\mu V)^2$; the darker color reflects lower power.

negative emotions. The studies described show that negative emotions can have contradictory influences on subjects' performance. In some cases, children manage to cope with the emotional experience and even channel it to exhibit better performance; however, in other cases, the efforts to regulate the emotional experience consume the available attentional resources and thus limit the child's ability to exert emotional self-regulation and continue to cognitively function. These findings highlight the fact that there are occasions that frustration and anxiety can have positive implications, especially when frustration is task related. It appears that, sometimes, losing a game, failing a test, or receiving negative feedback for performance can lead to exerting more effort and more focused task-oriented performance on the next try. It appears that parents, teachers, and clinicians who give children the opportunity to experience challenging and even frustrating experiences, while providing appropriate support, can promote children's recruitment of cognitive and emotional resources to exert better functioning. However, it was also shown that, for some of the children, challenging experiences are "too challenging" because the children experience extreme, negative emotions and, therefore, cannot channel their distress into better performance. Thus, there is a need for considering children's temperamental individual differences when required to cognitively function under stressful conditions. It appears that children with lower EC and higher NA will experience the same situation as much more negatively intense than children with more adaptive temperamental EC and NA tendencies. Although not always seen in behavior, children who tend to experience intense negative emotions – and are less able to soothe themselves and to regulate their emotional experience – can be less efficient in their performance. Educators and therapists must take into account that these children invest a lot of effort (as seen in larger brain activity during distress) to achieve results similar to those of children with higher EC and lower NA. As was also detailed, it appears that parents play an important role in modeling self-regulation for their children by continuing to function effectively even when the situation is frustrating and the expected outcomes are less favorable than desired.

CONCLUSIONS

This chapter incorporated extant literature regarding the importance of IC to children's cognitive and emotional development with the recognition that many daily situations involve negative emotional experiences.

Research shows that being overwhelmed with negative emotions affects a child's functioning, as expressed at the behavioral level and at the brain activity level. The literature also suggests that a child's ability to regulate an emotional experience is partly dictated by his/her temperamental characteristics, such as EC and NA. Parents, teachers, and clinicians should consider a child's individual temperamental differences, while providing developmentally appropriate situations for learning. We suggest a learning environment that includes challenges (which may also result in a negative emotional experience) accompanied by an authoritative approach that includes warmth and responsiveness as well as continued encouragement to achieve one's goals.

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EPILOGUE – DISTINCT MOTIVATIONS AND THEIR DIFFERENTIATED MECHANISMS: REFLECTIONS ON THE EMERGING NEUROSCIENCE OF HUMAN MOTIVATION

ABSTRACT

We reflect upon the histories of the behavioral science and the neuroscience of motivation, taking note of how these increasingly consilient disciplines inform each other. This volume's chapters illustrate how the field has moved beyond the study of immediate external rewards to the examination of neural mechanisms underlying varied motivational and appetitive states. Exemplifying this trend, we focus on emerging knowledge about intrinsic motivation, linking it with research on both the play and exploratory behaviors of nonhuman animals. We also speculate about large-scale brain networks related to salience processing as a possibly unique component of human intrinsic motivation. We further review emerging studies on neural correlates of basic psychological needs during decision making that are beginning to shine light on the integrative processes that support autonomous functioning. As with the contributions in this volume, such research reflects the increasing iteration

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between mechanistic studies and contemporary psychological models of human motivation.

Keywords: Autonomy; decision making; intrinsic motivation; PLAY system; SEEKING system; self-determination theory

The behavioral science of motivation has changed dramatically over its hundred-plus year history. Originally, the field focused on how events in the external environment could control behavior, either through drive reduction (Hull, 1943) or through conditioned rates of behavioral responding (Skinner, 1953). Subsequently, the field moved toward more nuanced issues of how behaviors are influenced by expectations of efficacy and control and moderated by individual differences (e.g., Rotter, 1954; Vroom, 1964). Still later researchers distinguished intrinsic and extrinsic motivation, based on the distinct properties of behaviors enacted spontaneously out of interest and curiosity relative to those performed for instrumental purposes (Deci, 1975; White, 1959). Still more recently evidence has shown that different qualities of motivation differentially impact behavioral performance, persistence and positive experience. Specifically, people's performance and experience is of the highest quality when they are autonomously motivated – that is when their actions fit with their reflectively held values and interests (Ryan & Deci, 2000, 2017). Each step forward in the field has brought a more complete understanding of human motivation, and more sophisticated predictive models that have real-world applicability.

Represented in the current volume we see parallel advances within the shorter history of the *neuroscience of motivation*. The "brain science" of motivation began, as did the behavioral field, by primarily focusing on those phenomena that are most easily operationalized in the laboratory – namely, the effects of externally administered incentives and punishments on brain and behavior. Standard reinforcement paradigms of course remain a reliable way of creating motivation in the laboratory to study its underlying mechanisms. But today, the neuroscience of motivation is field with an ever-growing toolbox of different neuroimaging and electrophysiological methods allowing researchers to localize the brain correlates and architecture of various motivational processes. Increasingly sophisticated techniques involving psychopharmacological manipulations and measurements of endogenous substances (e.g., hormones and neurotransmitter systems) are enabling researchers to decode the neurochemistries that fuel and regulate various aspects of motivation. Such methodological advancements undoubtedly hold great promise for unlocking previously inaccessible details about the nature of motivation in both humans and nonhuman animals.

Apart from its increasing methodological sophistication, just as the behavioral science of motivation evolved to encompass a wider expanse of motivational topics, the neuroscience of motivation is also increasingly addressing the complex problems that go beyond operant conditioning. Appreciation of cognitive, emotional, and psychological mediators has especially led to more complex views of the interconnectivity of motivational processes and their organization. Thus, chapters in this volume address individual differences in motivational propensities and in responses to reinforcement and feedback, the impact of choice and autonomy on motivational processes, and the different neural circuitries entailed in the organization and sustained energization of actions.

Accordingly, in our brief epilogue, we reflect upon the somewhat parallel histories of the behavioral science of motivation and the newer neuroscience of motivation, using exemplars from the current chapters. Each of these chapters focus on neurophysiological processes and systems that reflect various types of motivation that have been studied throughout the history of behavioral science, some since its earliest phases and others that have only more recently come into its spotlight. We also see that these chapters are often applying distinctions derived at the behavioral and experiential levels of analysis to formulate more differentiated hypotheses concerning the brain systems supporting these processes. In turn, neurophysiological distinctions are helping to clarify, refine, and delimit these psychological and behavioral models. This is what brings such excitement and creativity to this interdisciplinary interface. In this spirit, when reflecting upon chapter topics most relevant to our own research in self-determination theory (SDT; Ryan & Deci, 2000, 2017), we build upon the material covered in preceding chapters by reviewing complementary findings and by sharing some ideas for future research.

THE NEUROPSYCHOLOGY OF MOTIVATION AND ITS RELATIONS WITH BEHAVIORAL THEORIES

The empirical psychology of motivation is itself just over a century old. Yet during this history distinct paradigms have emerged that address different types of motivated behavior. We see in this volume multiple models in which neuropsychological research on motivation is building on or extending these earlier behavioral science perspectives.

Drive Theory

Foundational in the early research was experimental work in *drive theory* (Hull, 1943). Kringelbah and Berridge in the chapter “Neuroscience of Reward, Motivation, and Drive” of this volume argue, in fact, that it was the exploration of primary and secondary drives that provided early pathways into more differentiated motivation theories. In their view, it was the systematic testing, and yet ultimate failure, of homeostatic drive theory that led to its replacement of a more general conditioned reward theory.

Going beyond this general conditioned reward idea, Kringelbah and Berridge review a now well-established body of work that distinguishes between *wanting* and *liking*. Grounding this distinction is evidence of the partially dissociable circuits underlying each of these aspects of motivation, which are both part of the “pleasure cycle.” Thus, moving beyond simpler homeostasis hypotheses, they see more “carefully choreographed” dynamics in which both wanting (incentive salience) and liking (hedonics) play a role in both healthy and unhealthy behavioral energization and regulation. Particularly interesting in this dynamic is the potential for these appetitive and consummatory “modules” to become dissociated, so that sensitized wanting can motivate behavior independently of liking. Wanting, which is supported by the mesocorticolimbic dopamine pathways, can thus lead to motivated behavior that a person does not consciously desire, as seen in many addictive behaviors.

Operant Theory

Operant theory (Skinner, 1953) was a predominant force in thinking about motivation well after drive theory had faded. Focused on the functional relations between contingencies of reinforcement in the environment and behavior, experiments in this tradition have compellingly showed that, under controlled conditions, well-designed rewards and punishments can reliably motivate behavior. Although resisted by some operant theorists, in the 1950s researchers began to focus on person factors that might either mediate or moderate the effects of reinforcements on behaviors (e.g., Rotter, 1954). Rotter, in particular, argued that unless a person understands that there is a contingency between acting and receiving reinforcement there may be no motivation to act.

In the chapter "Neuroscience of Motivation and Organizational Behavior: Putting the Reinforcement Sensitivity Theory (RST) to Work," Corr, McNaughton, Wilson, Hutchison, Burch, & Poropat take this another step in their *Reinforcement Sensitivity Theory* (RST) of personality. They argue that many theories of motivation and management have a *Homo Economicus* idea of motivation in which individuals are always attempting to maximize external reward. Corr et al. suggest that this leads them to often ignore individual differences in reactions to workplace incentives. In particular, they suggest that pre-existing motivational dispositions conditioned by FFFS, BIS, and BAS sensitivities (Gray & McNaughton, 2000) alter the way in which individuals construe situations as "rewarding" or "punishing." That is, they emphasize that the manner in which events function as attractors and repulsors of behavior differs between persons. This recognizes the organismic component of motivation through external contingencies: situations only exert motivational pulls and pushes once their significance has been evaluated (Corr & McNaughton, 2012).

In this regard, we see the individual difference perspective articulated by Corr et al. as offering a potentially fruitful interface with our work in SDT, which has long been concerned with the *functional significance* of events as a determinant of autonomous and controlled forms of motivation (Ryan & Deci, 2000, 2017). Salient and negatively affective factors (e.g., threats and pressured evaluations) are known to exert deleterious effects on autonomous motives by conducing the experience of an external perceived locus of causality (deCharms, 1968). In light of the pre-existing motivational dispositions described by Corr et al., we may expect such factors to have more pronounced influences among people with higher FFFS and BIS sensitivities. Similarly, administrations of extrinsic tangible rewards, long known to undermine intrinsic motivation (Deci, Koestner, & Ryan, 1999), may be especially undermining for people higher in BAS sensitivity who are more susceptible to the seductive pull such affectively positive stimuli. Considerations such as these demonstrate how a neuropsychologically informed motivation science can stimulate new questions, even for already well-researched topics.

Laube and van den Bos in the chapter "Hormones and Affect in Adolescent Decision Making" also focus on differential sensitivity to rewards as a function of biological changes happening during adolescent development. They see a rapid change in gonadal hormone levels at pubertal onset as linked to motivational changes, especially increased "approach behavior," possibly mediated by changes in dopamine transmission. This stronger "reward approach" propensity is then associated with increased risk-taking and impulsivity seen during adolescence. They see the hormonal change as affecting reward-related regions, resulting in strong approach behavior, which in turn is hypothesized to account for increased risk-taking and impulsivity in adolescence. In fact so enthusiastic are they about the hormonal effects that they even advise against trying to teach adolescents how to cope. They state (p. xx):

> Clearly, if we want to reduce maladaptive behavior in teenagers, we should not aim at changing their nature by teaching them how to think differently. Telling them about the concrete risks of smoking marihuana and drunk driving or teaching them to think about future consequences of their current actions is unlikely to change their behavior in the future (Albert & Steinberg, 2011). Instead, we should rather focus on the context surrounding them and ensure that their environment matches their biological developmental state and capabilities.

They go on to recommend the merits of a full sleep cycle and setting limits on teens unhealthy and risky behaviors. Although we cannot agree with Laube et al.'s negative assessment of informational inputs to adolescents, or their strategies for intervention, we can agree that understanding how developmental changes impact behavioral propensities and decision making is a critical area for research.

Approach/Avoidance

Corr et al.'s distinctions about reward sensitivity and its relations with FFFS, BIS, and BAS raise the more general issue of approach and avoidance motivation systems in motivational studies. Approach and avoidance distinctions have been important with in the behavioral science of motivation, especially goal theories, for some time (Atkinson, 1958; Elliot, 1999).

The neuroscience of this topic is directly the concern of Angus and Harmon-Jones in the chapter "On the Neuroscience of Approach and Withdrawal Motivation, with a Focus on the Role of Asymmetrical Frontal Cortical Activity." They focus on approach and avoidance as lateralized brain activity, citing now decades of evidence that asymmetrical leftwards activity in the frontal cortex is functionally associated with *approach motivation*, whereas rightwards asymmetrical activity is functionally related to *withdrawal motivation*. At a state level, they report that exposure to conditions that produce approach or withdrawal are associated with an increase in left or right hemispheric asymmetry, respectively. Reciprocally, producing increases in cortical asymmetry can also directly enhance approach or withdrawal motivation. Among the myriad implications of this work are that manipulations known to induce asymmetrical activation in the frontal cortex can be seen to influence approach-related emotions (e.g., anger, proactive aggression) in social situations.

Effort and Energization

Understanding just when and how organisms allocate energy and organize efforts toward particular goals is among the central problems in motivation. Salamone and Correa ("Neurobiology of Effort and the Role of Mesolimbic Dopamine") argue that one way to approach this problem is through examining motor behavior. They highlight the high degree of overlap between what has been studied as "motor control" and the activational aspects of motivation. They further suggest that there is functional overlap in neural systems as well (Salamone, 2010). Here, they particularly point to the role of mesolimbic dopamine not only in behavioral activation, but also in effort-related decision making and choices. Individual differences in dopamine transmission in, for example, the striatum and ventromedial prefrontal cortex affect people's willingness to expend effort. Such effects can also be experimentally demonstrated using methods such as the administration of tetrabenazine (e.g., Nunes et al., 2013; Yohn et al., 2015). This opens up promising possibilities for identifying drugs that might ameliorate disorders associated with disturbances in the regulation of effort.

One important point of Salamone and Correa's et al.'s chapter, as well as several other chapters in this volume, is underscoring that the functional overlap of neural systems is great. Their research shows that dopamine is not just part of a "pleasure system" but is intertwined with many aspects of motivation, including effort mobilization. This is a recurrent theme in this volume – the more we differentiate the elements of motivation we study, the more we see their dependence on interconnectivities between brain areas that serve multiple functions.

On to Intrinsic Motivation

By the late 1950s, behavioral scientists had discovered the limits of motivation theories that were based entirely on external reinforcement paradigms. As White (1959) underscored, the behavioral paradigms at the time were failing to explain phenomena like curiosity, play, and learning out of interest that seemingly defied reduction to external rewards and punishments. He introduced the concept of effectance motivation as an inherent psychological propensity, which became the forerunner of the construct of intrinsic motivation as used in SDT. The recognition of intrinsic motivation brought with it a view that people, and many other animals (Ryan, Kuhl, & Deci, 1997), are *active organisms* with spontaneous strivings to explore and actively engage with the objects, people, events, and ideas of their world (Ryan & Deci, 2000, 2017).

Human intrinsic motivation has only recently attracted the empirical efforts of researchers employing neuroscience methods. However, just as the earliest studies on intrinsic motivation were done with nonhuman primates (Harlow, 1950), the first insights into the neural bases of intrinsic motivation have come from research on nonhuman animals. Perhaps most prominent in this regard, Panksepp and colleagues have argued that mammals are hardwired for social play of the rough-and-tumble (R&T) variety (Panksepp, 1998; Panksepp & Biven, 2012). They postulate the existence of a subcortical PLAY system that is comprised at least in part by midline thalamic regions. The parascicular complex and posterior dorsomedial thalamic nuclei, for example, process the sensory (i.e., touch) information that appears to instigate R&T play in rats, and lesions to these areas diminish the animals' the intrinsic desire to play. Humans, of course, are capable of more cognitively sophisticated forms of play, but Panksepp and colleagues argue that human play is a cortical elaboration of basic play urges energized by subcortical mammalian PLAY circuitry.

Even among nonhuman animals, evidence suggests that play has unconditionally rewarding properties. In the laboratory, animals will learn instrumental tasks for opportunities to play and rats have been found to produce ultrasonic 50 kHz chirps during bouts of play that are similarly emitted during other types of pleasurable activities. A body of evidence implicates endogenous opioids in the hedonic ("liking") components of play, though many neurochemical systems have been found to yield specific effects on play (Trezza, Baarendse, & Vanderschuren, 2010). From both evolutionary and developmental perspectives, play can be seen to confer many adaptive consequences for social animals, helping them to develop various physical, cognitive, and social capacities. At the experiential level, however, play is fun and enjoyed for its own sake.

The behaviors and emotions that characterize play are distinct from those that characterize exploratory behaviors marked by interest and curiosity. This class of intrinsically motivated behaviors has also been characterized in nonhuman animals by the operation of the so-called SEEKING system, which Panksepp and colleagues describe as a "general-purpose system for obtaining all kinds of resources that exist in the world, from nuts to knowledge, so to speak" (Panksepp & Biven, p. 104). This SEEKING terminology is an alternative to other labels that have been used to describe the operation of this motivational system (e.g., Gray's BAS; see the chapter "Neuroscience of Motivation and Organizational Behavior: Putting the Reinforcement Sensitivity Theory (RST) to Work") and was chosen to emphasize the energized positive affect and invigorated exploratory attitude that it arouses. More importantly, Panksepp's SEEKING terminology is intended to portray animals as active agents "as opposed to simply passive information-processing machines, as classical behaviorism and modern information-processing approaches have envisioned" (Panksepp & Northoff, 2009, p. 194).

Panksepp and Biven (2012) describe the SEEKING system as being comprised of the ventral tegmental area (VTA), the nucleus accumbens (NA), the VMPFC, and the dopaminergic projections arising from the VTA that innervate these areas. Some of the chapters included in the present volume have addressed aspects of the SEEKING system, albeit from alternative perspectives. For example, Kringelbach and Berridge ("Neuroscience of Reward, Motivation, and Drive") described the operation of this system in their distinction between *wanting* and *liking* – it is the eager appetitive phase of the pleasure cycle that reflects the operation of the SEEKING system. Salamone and Correa ("Neurobiology of Effort and the Role of Mesolimbic Dopamine") also point to the general importance of this system in behavioral activation and effortful exertions. Although components of the SEEKING system do function as a "reward network," Panksepp and colleagues argue that this system has a broad role as an energizer of exploratory behaviors, including the "many mental complexities that humans experience as persistent feelings of interest, curiosity, sensation seeking and, in the presence of a sufficiently complex cortex, the search for higher meaning" (Panksepp, 1998, p. 145).

Consistent with the idea that the SEEKING system subserves intrinsic motivation, in the chapter ""Your Choice" Motivates You in the Brain: The Emergence of Autonomy Neuroscience," Murayama, Izuma, Aoki, and Matsumoto review neuroimaging studies showing that affordances for autonomy (e.g., choice), known to facilitate the expression of intrinsic motivation (Ryan & Deci, 2000, 2017), are processed by structures that represent this system in humans. For example, in one study Murayama, Matsumoto, Izuma, and Matsumoto (2010) showed that the undermining effect of performance-based monetary rewards on intrinsic motivation is correlated with diminished activity in the midbrain and striatum. Further evidence is presented in the chapter "Insular Cortex Activity as the Neural Base of Intrinsic Motivation," where Lee reviews other neuroimaging studies that again implicate key structures that comprise the SEEKING system in the support of intrinsic motivation.

Lee also reviews an exciting set of fMRI studies that identify activities within the anterior insula (AI), and its connectivity with striatal regions, as a possibly unique component of intrinsic motivation. Although the insula is one of the most commonly activated structures in all of neuroimaging research (Menon & Uddin, 2010), we find the involvement of the AI in intrinsic motivation particularly interesting for two reasons. First, the AI has undergone great expansion in humans and most aspects of the human insula have no structural equivalent in the rat or monkey brain (Craig, 2009). It is possible then, that the AI may support the more cognitively complex processes that characterize human intrinsic motivation. Second, connectivity analyses of fMRI recordings have identified the AI to be a crucial node in what is called the "salience network" (SN), an assembly of regions that also includes the dorsal aspects of the ACC (Menon, 2015; Menon & Uddin, 2010). The SN is believed to help focus the "spotlight of attention" to subjectively important events and to mobilize neural resources in the service of goal-directed behavior. Most relevant here is the suggestion (Menon, 2015; Menon & Uddin, 2010) that the AI is a dynamic hub for modulating activity between the so-called "default mode network" (DMN), whose regions include the VMPFC and the posterior cingulate cortex, and "central executive network" (CEN). Regions of the DMN show high levels of activity during passive resting states and during tasks involving self-focused cognition (Gusnard & Raichle, 2001; Northoff et al. 2006), but during cognitive demanding tasks, activity within the DMN is suppressed as CEN activity increases.

The findings reviewed in the chapter "Insular Cortex Activity as the Neural Base of Intrinsic Motivation" of greater AI activity during intrinsic motivation may thus suggest enhanced salience processing and deployment of the CEN during intrinsic motivation, which may also help account for its performance enhancing properties. This idea is also consistent with the findings of Kang et al. (2009) and Murayama et al. (2010), who report greater activations in lateral PFC regions during intrinsic motivation, and with Ulrich et al.'s (2014) findings of increases of activity within left inferior frontal gyrus and concomitant decreases within the MPFC regions during intrinsically motivated flow states. Given these interesting, albeit preliminary findings, we believe that investigating AI-mediated switching between large-scale brain networks offers a promising future avenue for examining both the neural correlates of intrinsic motivation and the neurophysiological processes through which it enhances behavioral performance.

The chapter “Motivated Cognition: Neural and Computational Mechanisms of Curiosity, Attention, and Intrinsic Motivation” by Gottlieb, Lopes, and Oudeyer turns us in the direction of psychological satisfactions that carry inherent rewards. Gottlieb et al. argue for a unified theory of curiosity as a form of motivated cognition. They propose that curiosity consists of a set of mechanisms associated with novelty, surprise, and “drives” based on reward and uncertainty reduction. They also suggest that there may be “self-directed metacognitive processes” that contribute. These mechanisms presumably evolved to allow individuals to uncover the useful regularities in their environments – to discover how things work. This set of mechanisms thus functions to steer the organism toward niches of maximal learning, and away from both non-optimally random and highly familiar, quite predicable, activities. Here, then is recognition that we have evolved to be curious, with both pushes and pulls underlying that propensity.

The chapter “The Role of Feedback in Learning and Motivation” highlights yet another intrinsic type of reward – namely, the satisfaction associated with competence feedback. In that chapter, Tricomi and DePasque point out just how important performance feedback is in the guidance of learning. They further suggest that even when feedback itself has no extrinsic value, it can produce subjective feelings similar to “rewards” and “punishments.” Therefore, feedback can play both an informative and a motivational role. Tricomi and DePasque then highlight how neural circuits that process reward value involving regions of dopaminergic input (e.g., striatum and VMPFC) can be activated by performance feedback even in the absence of extrinsic reward. Moreover, the effects of feedback on dopaminergic reactions are often moderated by motivational context. For example, whether learners are oriented toward the informative versus evaluative (controlling) aspect of feedback, and whether individual learners are motivated toward mastery versus performance goals can effect how feedback impacts striatal and VMPFC circuits.

Murty and Dickerson focus in the chapter “Motivational Influences on Memory” on how motivation influences learning and memory, and they particularly look at different phases of memory are affected by incentives and engage different neural systems. They first review data on how motivation, including external rewards, can enhance episodic memory. Pertinent to intrinsic motivation, they argue further that such reward effects are not restricted to extrinsic monetary rewards. Findings indicate, in fact, that much of the same neural architecture is activated during intrinsically motivated learning, such as learning from curiosity. Intrinsic rewards can significantly engage mesolimbic dopamine circuitry and thereby promote enhanced learning. Thus Murty and Dickerson propose that harnessing intrinsic rewards have great potential in classroom settings, especially as they energize both encoding and consolidation phases of the learning process.

From Intrinsic Motivation to Autonomy

Within the behavioral science of motivation a further change occurred subsequent to the distinction between intrinsic and extrinsic motivations. One characteristic of intrinsic motivation is that it is highly volitional – people report high sense of autonomy, willingness, and self-motivation when intrinsically motivated. But it is also true that many non-intrinsically motivated behaviors are done with a high sense of volition or autonomy. In fact a good deal of research from SDT (Ryan & Deci, 2000, 2017) has pointed to the very different motivational characteristic of autonomous versus controlled motivations. Autonomous motivations are those in which the person experiences a sense of willingness and choice in acting, whereas controlled motives are those stemming from internal pressures or external controls that are not accompanied by this sense of choice or willingness.

In ""Your Choice" Motivates You in the Brain: The Emergence of Autonomy Neuroscience," Murayama and colleagues peek into this phenomenon of autonomy and sense of choice as it relates to motivational consequences. They review the scant, but growing, body of research on the neural correlates of personal choice. They especially focus on evidence that people value opportunities to exercise personal choice, that making choices influences people's perceptions and preferences, and that choice enhances people's motivation and performance when it supports their abilities to autonomously self-regulate. Although the phenomenon of personal choice is complex, research does suggest again that the striatum and the VMPFC may play a critical role in motivational processes elicited by opportunities to exercise personal choice. More generally, Murayama et al. encourage future research programs to address this new realm of "autonomy neuroscience."

We suggest that the utility of an autonomy neuroscience is further underscored by studies showing that different brain networks are recruited by two broad classes of decision-making. In a recent review, Nakao, Ohira, and Northoff (2012) differentiated experimental paradigms for *externally guided* decision making from those for *internally guided* decision making. In the laboratory, externally guided decision-making scenarios are multiple choice tasks that contain at least one objectively correct response and require people to choose with some degree of uncertainty. For example, Nakao, Bai, Nashiwa, and Northoff (2013) presented participants with pairs of occupation-related words and asked them to select the option that is more frequently used in the English language. Internally guided decision-making scenarios, by contrast, are multiple choice tasks that preclude objectively "right" or "wrong" choices and instead challenge people to choose of the basis of subjective criteria. In the same study, Nakao et al. asked participants to choose among the word pairs the occupation they would prefer as a possible career.

In a meta-analysis, Nakao et al. (2012) found that these two broad types of decision-making processes preferentially recruit neural regions that overlap with the distinction between the CEN and the DMN, with internally guided decision making being associated with activity within the DMN structures. The involvement of the DMN structures during internally guided decision making is intriguing for an autonomy neuroscience because this network is reliably engaged by tasks that involve self-referential cognitive processes (Northoff et al., 2006). Of particular relevance is the VMPFC, which has been proposed to play an important role in recruiting the self-knowledge representations that are used to regulate conflicts during personal decision making (Nakao et al., 2009, 2010). Also relevant are regions within the ACC, which in other work have been characterized as a cortical extension of the septo-hippocampal BIS (Corr et al. "Neuroscience of Motivation and Organizational Behavior: Putting the Reinforcement Sensitivity Theory (RST) to Work") involved in the production anxious uncertainty elicited by decisional conflicts (Hirsh, Mar, & Peterson, 2012).

Against the backdrop of Nakao et al.'s findings, we have begun to use decision-making paradigms to elucidate the neural systems that support *integrative processes*, which refer to people's constructive tendencies to engage with psychological conflicts and develop and act from a coherent sense of self (Ryan, 1995; Weinstein, Przybylski, & Ryan, 2013). Integrative processes are crucial for autonomous functioning because they concern how people clarify their core values, focus and prioritize their life goals, and accordingly make decisions that are congruent with their abiding sense of self. One way that SDT differs from both classic (e.g., Freud, 1927; Loevinger, 1976; Rogers, 1951) and more contemporary (e.g., Kuhl, 2000;

McAdams, 2013) perspectives that similarly recognize the importance of self-integration is that it specifies and emphasizes the role basic psychological needs for competence (feeling effectual), relatedness (feeling connected with others), and autonomy (feeling volitional) in facilitating the expression of people's integrative tendencies (Ryan, 1995; Ryan & Deci, 2000, 2017).

In this vein, Di Domenico, Fournier, Ayaz, and Ruocco (2013) used functional near-infrared spectroscopy to examine how individual differences in need fulfilling experiences relate to the activity of regions within the VMPFC (Brodmann area 10) during the regulation of internally guided decision-making conflicts. As Ryan et al. (1997) argued early on, integrated functioning entails the use of self-knowledge inputs to guide choice behavior. Situations of varying degrees of decisional conflict thus offer a means to test people's integrative capacities. Using an occupational choice task similar to Nakao et al. (2013), Di Domenico et al. (2013) had young adults make a series of forced choices (e.g., Which occupation would you prefer, dancer or chemist?) that required them to access their self-knowledge (i.e., preferences, goals, and values). Importantly, the degree of decisional conflict was manipulated on the basis of participants' unique preference ratings for the word stimuli, which were obtained prior to neuroimaging. While low-conflict situations involved deciding between an attractive and unattractive occupation, high-conflict situations involved deciding between two similarly attractive or unattractive occupations.

Di Domenico et al. (2013) found that people reporting higher need fulfillment in their day-to-day experiences exhibited a pattern of reaction times and VMPFC activity suggestive of enhanced integrative processing. Specifically, they evidenced a discriminating pattern of VMPFC activity, mobilizing greater neural resources in high- relative to low-conflict situations. On the other hand, people reporting lower need fulfillment evidenced levels of VMPFC activity that poorly distinguished the decision-making situations. These results are consistent with the idea that need fulfillment is associated with enhanced use of self-knowledge when confronting decisional conflicts.

Using the same decision-making paradigm, Di Domenico, Le, Liu, Ayaz, and Fournier (2016) extended these initial findings using EPRs to examine how experiences of need fulfillment relate to ACC activity during conflict regulation. While the VMPFC is believed to play an executive role during internally guided decision-making, recruiting self-knowledge representations that are used to bias choice behavior, the ACC is believe to play an evaluative role, monitoring conflicts during information processing and signaling the demand for stronger self-knowledge inputs to guide efficient, self-congruent decision-making. In this study, people reporting higher need fulfillment evidenced larger *conflict negativity* amplitudes, an electrophysiological measure of conflict processing within the ACC (Nakao et al., 2013). These complementary findings suggest that need fulfillment not only increases people's readiness to bring their self-knowledge to bear on decisional conflicts, it also increases their receptivity to and open processing of conflict-laden situations in the service of self-congruent decision-making. More broadly, these initial findings carry important implications for autonomy neuroscience, as they demonstrate that structures within the DMN network are modulated by experiences of need fulfillment during internally guided decision making.

Developing Motivational Capacities for Self-Regulation and Autonomy

Fabiash et al. (Children's Inhibitory Control when Facing Negative Emotions) focus on executive functions, and particularly inhibitory control (IC; e.g., withholding prepotent responses) and effortful control (EC; e.g., focusing attention, shifting sets). They note how functions concerning inhibition and effort allocation are susceptible to disruption by emotional experiences. Particularly negative emotion influence capacities for response inhibition, as indexed especially by higher N2 amplitudes in the ERP work they review. Both temperament and negative affectivity impact these functions. So does the social environment. Parents who are more responsive to their children's emotional states help them learn ways to cope with emotional experience before it gets out of control. In contrast, controlling styles of parenting and harsh maternal discipline has been associated with low levels of IC in children (Moilanen, Shaw, Dishion, Gardner, & Wilson, 2010). Consistently, maternal and paternal harsh, negative controlling discipline strategies (e.g., physical punishment, denial of privileges) have been associated with lower levels of EC in children (Karreman, van Tuijl, van Aken, & Deković, 2008).

This dovetails with a growing body of research within SDT pointing in the same direction. For example, Bernier, Carlson, and Whipple (2010) coded mother-child interactions when children were between 12 and 15 months at the time, and then assessed children's executive functioning (i.e., working memory, impulse control, set shifting) at 18 months, and again at 26 months. Maternal autonomy support was a strong predictor of the children's executive function at each point in time, even stronger than mothers' sensitivity. More recently Bindman, Pomerantz, and Roisman

(2015) showed that parents who were high in autonomy support during the first three years of their children's lives had children who displayed stronger *executive function* (e.g., effective inhibition, sustained attention, delay of gratification) a year or two later. This early autonomy support further predicted children's subsequent achievement in elementary and high school, a relation that was mediated by executive functioning.

One particularly controlling disciplinary technique is parental *conditional regard*, which refers to parents' withholding of their approval and affection when their child fails to meet their standards of excellence (Ryan & Deci, 2017). This type of parental control thus turns the basic psychological needs for autonomy and relatedness against each other. In recent set of papers, Huffmeijer and colleagues report on studies using ERPs to examine the neural correlates of conditional regard using facial stimuli. In one study on a sample of young adult women, Huffmeijer, Tops, Alink, Bakermans-Kranenburg, and van IJzendoorn (2011) found that maternal love withdrawal was associated with larger vertex positive potentials (VPP), suggesting a heightened processing of emotional facial expressions. Interestingly, participants reporting greater maternal love withdrawal evidenced more pronounced VPP amplitudes in response to disgusted versus happy facial expressions, suggesting that such facial expressions particularly threatening or perhaps relevant to them. Higher levels of maternal love withdrawal were also associated with larger N400 amplitudes in response to performance feedback on a flanker task presented with incongruent emotional expressions (e.g., positive feedback coupled with disgusted expressions). This latter finding is consistent with the idea of a tight connection between performance and relational feedback among people experiencing higher levels of conditional parental regard. In a follow-up ERP study, Huffmeijer et al. (2013) found that intranasal oxytocin administrations augmented the processing of facial expressions, but to a lesser degree in participants reporting higher levels of maternal love withdrawal. The results of study may thus suggest that parental conditional regard may result in alterations of oxytocin system, which is implicated in regulation of positive social behaviors.

Such evidence also connects with research reviewed by Tops, Montero-Marín, and Quirin in the chapter "Too Much of a Good Thing: A Neuro-Dynamic Personality Model Explaining Engagement and Its Protective Inhibition," who focus on two primary motivational systems: what they call *predictive* and *reactive* control systems (PARCS). The predictive system is adapted for secure environments, whereas the reactive system focuses attention narrowly on the local situation, and is adapted for less certain environments. Processes associated with flexible predictive control are those most closely associated with autonomous self-regulation. Like Farish et al., Tops et al. see the emergence of these flexible predictive capacities as dependent on extended parental investment and caring, through which the child becomes less rigidly controlled by the environment and more in tune with possibilities for action and gratification. By contrast, reactive control is driven by immediate and pressing environmental demands. Both chapters "Too Much of a Good Thing: A Neuro-Dynamic Personality Model Explaining Engagement and Its Protective Inhibition," and "Children's Inhibitory Control when Facing Negative Emotions" thus speak to how nurturance and psychological need support are important in shaping the predominance of different mechanisms underlying types of motivation.

Summary and Observations

The behavioral science of motivation moved from relatively simple views of behavior as being controlled by external rewards to a more complex view that there are multiple types of motivation, each with different characteristics, antecedents and consequences. Some behaviors are very much conditioned and controlled by environmental cues; others more mediated by intentions and choice. The neuroscience of motivation has similarly grown in the complexity of its views. Early conceptions of behavior being driven by a "reward center" in the brain have been replaced by the idea that there are multiple brain systems implicated in the organization of behavior, and their interplay in part corresponds to the varied forms of motivation we observe in behavior. Some behaviors can be underpinned by wanting without liking, some by flexible regulation others by rigid controls. Some individuals are highly responsive or disposed to rewards affects, others more impervious. Understanding of these individual differences and dynamic effects has been rapidly advanced by differentiations offered at the mechanistic level.

Another lesson from surveying these diverse contributions is our increased understanding of the multiple functions played by neural circuits. For instance, we have seen how dopamine transmission plays a role in multiple processes from feedback salience to effort allocation. Increasingly, it is clear that we are moving form an attempt to localize functions, to understanding that most psychological and behavioral phenomena reflect systematic interconnections that differentially involve overlapping areas of the brain. Perhaps most straightforwardly we can see in this volume that we have moved well beyond the era where explanations of behavior were either psychological or neurological. What we see is that psychological and behavioral phenomena can be coordinated with our understanding of mechanisms, and informed by our measurement of brain processes in real time. Reciprocally, much of what is manifest in the brain is occasioned by the social and psychological conditions in which individuals finds themselves. The excitement of the new neuroscience of motivation is that it is indeed an iterative field aiming toward consilience.

Richard M. Ryan
Stefano I. Di Domenico

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