CHAPTER 7

Motivational Influences on Cognitive Control: A Cognitive Neuroscience Perspective

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ABSTRACT

Motivation is an important component of self-regulation that helps set the effort level an organism is willing to expend to achieve a desired goal. However, motivation is an elusive concept in psychological research, with investigations typically targeting either very macro-level (e.g., effects of personality individual differences and experimental manipulations on global behavior) or very micro-level (e.g., physiological interventions targeting specific brain structures) processes. Thus, the current state of knowledge is very poor regarding the particular mechanisms by which motivation influences cognitive and neural systems to drive changes in specific components of behavior. This chapter reviews major perspectives on motivation arising from both the social-personality and neuroscience literatures, and then discuss how a cognitive neuroscience perspective might be fruitfully applied to fill the gaps between them. Specifically, the chapter reviews literature, including our own recent work, that suggests motivational manipulations impact brain regions associated with the exertion of specific cognitive control functions. The chapter concludes by outlining unresolved questions in motivation, and by suggesting directions for future progress in this domain.

Keywords: Dopamine, nucleus accumbens, basal ganglia, prefrontal cortex, orbitofrontal cortex, insula, amygdala, anterior cingulate cortex, reward, punishment, affect, incentive salience, individual differences, working memory, attention

MOTIVATIONAL INFLUENCES ON COGNITIVE CONTROL: A COGNITIVE NEUROSCIENCE PERSPECTIVE

Self-control involves bringing behavior in line with goals. Given that achieving one goal may preclude pursuing another, it is important to be able to prioritize competing goals, and allocate resources accordingly. We suggest that motivation is a central component of self-control, as it involves weighing benefits and costs of actions, deciding which course of action is most appealing, and setting effort levels in accordance with the value of the eventual goal. Importantly, motivational influences are not only of interest in the study of overt behavior, but have begun to be investigated in terms of their effects on cognition, such as learning and performance strategies and cognitive control processes (e.g., *see* Markman, Maddox, & Baldwin, 2005). The interaction between motivational and cognitive control systems is a key area of interest, as cognitive control resources, such as sustained attention, are costly but potentially useful self-regulatory mechanisms that can be brought to bear on task performance, given enough incentive to outweigh the costs. This chapter argues that the cognitive neuroscience approach, with its ability to bridge different levels of explanation and analysis–neurobiological, cognitive, behavioral, individual differences, and social-psychological–is well-suited to the study of motivation, and hence to gaining a more thorough understanding of self-control.

Although motivation has been the subject of psychological research for decades, there is not a consensus on what its core features are. Motivation is often described generally as the internal drive to act, as if it were a force of its own, akin to the concept of will. However, this vague definition ignores the complex chain of computations that take place when individuals perceive opportunities for either rewarding or aversive outcomes, and change their behavior to attain or avoid them. Part of the reason that motivation is such a complex subject to grasp is that it has been investigated from a number of different perspectives, and often, researchers have worked in parallel at different levels of analysis without endeavoring to link their work to other areas. Therefore, the aim of this chapter is not only to review the main findings within separate disciplines, but also to draw connections where possible.

The main sections of the literature review will look at the contributions of social and personality psychologists, neuroscientists, and finally the emerging work of cognitive neuroscientists, all of whom are interested in motivation, but are asking and answering different kinds of motivation-related questions. Social and personality psychologists ask how individuals are, or fail to be, motivated in different situations. Who are the people that come into the lab to participate in experiments, and how do their thoughts, goals, and personalities affect their motivation? Neuroscientists study the other end of the spectrum to ask how the brains of animals and humans process stimuli associated with rewards and punishment. Finally, the cognitive neuroscience approach to motivation focuses on the cognitive and neural mechanisms that underlie individuals' ability to enact behavior that matches their goals and motivations. Following the sections reviewing these three areas, a final section attempts to integrate these disparate views of motivation.

SOCIAL AND PERSONALITY PERSPECTIVES

Social and personality psychologists argue that both individual variables, such as goals, affect, self-image, and personality, and task variables, such as the framing and social context, interact to influence the kind of rewards and punishments that will influence motivation at a high level. This body of research demonstrates that knowledge about individual differences can provide greater explanatory power to understand task behavior than can approaches that examine only average group responses. Various theorists from within this tradition have provided accounts of motivation that attempt to specify the nature of the interaction between goals, self-image, personality, and motivation.

Carver and Scheier view motivation as arising from the activity of feedback loops, using the individual's goal value as the set point, and working to reduce discrepancies between the current state and the goal value (Carver, Sutton, & Scheier, 2000). A second level in the feedback system monitors progress toward the goal value, and it is this rate of progress that influences affect. Positive affect occurs when the system detects greater progress toward the goal than expected. Conversely, negative affect occurs when less than expected progress is detected. No change in affect occurs when goal progress matches the expected value. Thus, when individuals have a goal in mind, there is a monitoring system linked to emotion that can exert influence to prompt increased effort if progress is not adequate. In this scenario, affect itself is part of the reinforcement process, and thus is a core component of motivational drive.

Goals are clearly an essential part of motivational processes, but goals are heterogeneous by nature. The intentions that people form in response to tasks can vary, and the type of intentions individuals have can affect the likelihood of success. Gollwitzer (1999) has postulated two distinct types of intention: goal intentions and implementation intentions. Goal intentions are focused on the end-point, the achievement of a particular outcome that is desired, such as getting a good grade on a test. Implementation intentions, by contrast, are focused on how the task is going to be accomplished, and have specific external cues associated with them—for example, after I get back from the cafeteria, I am going to study for the test by looking at the sample exam questions in the book. By breaking a larger goal intention down into the subset of activities that need to be done to reach it, and by setting environmental triggers, individuals who set implementation intentions achieve higher rates of goal attainment than individuals who do not (Gollwitzer, 1999).

Taking one step back from the structure of goals, it is necessary to ask what factors affect how goals are selected in the first place. One answer is that individuals' prediction of affect (affective forecasting) can be a motivator to engage in a task—that is, individuals may choose to take part in a task because they predict that the task's reward will make them feel happy (Gilbert & Wilson, 2000). Thus, the affective response that is generated when the person is thinking about the reward is taken as a predictor of what the actual reaction to the receipt of the reward will be. Gilbert and Wilson (2000) have suggested that this prediction can be inaccurate for a number of reasons, leading to the phenomenon of "miswanting"-wanting something that is not liked, or enjoyed, when actually received. For example, if people are in a particularly good mood when evaluating a reward, it may lead to an overestimation of how happy it will make them in the future, because they base this prediction on how they feel at the moment they are thinking about the reward.

Expectancy is an important variable in motivation, and not only where predictions of future happiness are concerned. According to Bandura's Self Efficacy Theory, individuals' confidence in their ability to accomplish a task at hand can affect their motivation to engage in it, and the effort they put forth (*see* Bandura, 1997). Bandura distinguishes between outcome expectations, the consequences of achieving versus not achieving a goal, and efficacy expectations, the competency with which individuals expect to pursue those goals. These factors are related, in that a high level of efficacy expectation usually results in a high outcome expectation. For example, a student with a high sense of academic efficacy may expect opportunities for good jobs in the future. However, high efficacy does not always lead to high outcome expectation, if the student in the aforementioned example is going into a field with relatively few available jobs.

Another important component of social and educational psychological theories is the distinction between intrinsic motivation, positive feelings engendered by performing a task per se, and extrinsic motivation, where performance on a task is reinforced in some way, such as by money, food, points, or verbal praise. For example, this distinction has played a key role in Deci & Ryan's Cognitive Evaluation Theory (CET; Deci & Ryan, 1985). According to CET, extrinsic incentives can be effective at improving performance, but ultimately harm intrinsic, or "authentic" motivation because they are perceived as controlling behavior and limiting autonomy. Participants are able to explain their engagement and effort on a task as caused by desire for the external reward rather than by their own intrinsic interest, even if the task was inherently interesting to them at the outset. Thus, adding incentives to a task has the potential to diminish, or even eliminate, intrinsic motivation.

Although this theory has been influential in motivation research and particularly in education, it is also controversial. Results of multiple meta-analyses by Cameron and colleagues (Cameron, 2001; Cameron & Pierce, 1994) showed that in general, rewards for good performance do not harm intrinsic motivation. Rather, a small subset of incentives was found to be harmful—namely, non-performance-contingent rewards, or rewards offered for mere participation rather than performance that met some criterion. This effect is only present when these non-performance-contingent rewards are expected, not when they are unexpected. Thus, harmful effects only occur for rewards offered in advance just for engaging in a task. In addition, verbal praise was found to increase intrinsic motivation.

In many of Deci & Ryan's experiments, intrinsic motivation is measured by time spent on the task in a free-choice situation. The choice of what activity to engage in is an important aspect of motivation, as is the type of goals individuals have when they engage in tasks. Performance goals involve a focus on how well an individual will do at a task in relation to others, with an emphasis on appearing competent. In contrast, mastery goals emphasize the mechanics of learning to do the task well, and gaining skill and competence (Dweck, 1986). Elliot and colleagues have further proposed breaking down performance goals into performance-approach and performance-avoidance goals, involving appearing competent in front of others or not appearing incompetent, respectively (Elliot, McGregor, & Gable, 1999). Mastery goals have been associated with greater intrinsic interest in the task (e.g., Harackiewicz et al., 1997), greater persistence and effort (e.g., Elliot et al, 1999) and greater likelihood of choosing challenging tasks over excessively difficult or trivially easy tasks (Atkinson & Raphelson, 1956). Nevertheless, adopting mastery goals has not been consistently related to better performance, perhaps because individuals who are interested in a subject are more likely to seek out related interesting information that is not instrumental to better performance, and thus aren't as focused (Elliot et al., 1999). Rather, performance-approach goals seem to be most consistently related to better performance.

The next step after selecting goals is to work toward attaining them. How successful individuals are at achieving their goals may depend on their "motivational skills," which comprise the resources people have available to dedicate towards goal pursuit and task persistence (Heggestad & Kanfer, 1997). Unlike personality characteristics, which are presumably immutable, these skills may be developed over time. A related idea is the concept of active self, a resource used to inhibit actions that are tempting or habitual, initiate action, and make deliberate, conscious choices (Baumeister, Muraven, & Tice, 2000). According to this theory, self-control is a severely limited resource, and can be depleted by even short periods of engagement (i.e., <5 minutes). For example, when participants were asked to eat radishes and refrain from eating readily accessible cookies they persisted less on subsequent unsolvable geometry problems (Baumeister, Bratslavsky, Muraven, & Tice, 1998). This temporary depletion is associated with subsequent poorer performance on a wide range of tasks that require active self, from persisting on unsolvable problems to continuing to hold handgrip bars together (Baumeister et al., 1998, 2000; Muraven, Tice, & Baumeister, 1998). Such rapid depletion of self-control is problematic in that many everyday activities seem to require the engagement of an active self. Muraven & Baumeister (2000) suggest that a solution to this problem is to consider the active self as analogous to a muscle, in that it quickly tires from exertion, but can return to strength with rest. In addition, the frequent exercise of self-control can cause an increase in the amount of available resource and the length of time it can be engaged.

Whereas social psychology theories of motivation focus on situational factors such as how incentive structures influence motivation, personality theories look at the traits people have that influence their motivation. One classic distinction is the tendency towards approach (seeking rewards) vs. withdrawal (avoiding punishment). An influential personality theory dealing with approach and withdrawal is Jeffrey Gray's Behavioral Inhibition/Activation System (BIS/BAS), which posits that trait tendencies toward inhibition or activation are major determinants of behavior (Gray, 1970, 1981). The BAS system is related both to approach of rewarding stimuli, and active escape from negative stimuli. As such, it encompasses both positive affect in the sense of joy from receiving a reward, and relief at escaping a punishment. The BIS system is associated with a suspension of activity (freezing behavior), and encompasses both negative feeling of punishment, fear, and the loss of a potential reward, sadness/disappointment. The theory conceptualizes affect as a single bipolar dimension, running from negative to positive.

By contrast, Carver and colleagues (e.g., *see* Carver, Sutton & Scheier, 2000) view affect as two orthogonal dimensions, positive affect and negative affect. Low positive affect is characterized by sadness, and high positive affect by joy, whereas low negative affect is characterized by relief, and high negative affect by anxiety. Carver and White (1994) developed a scale to assess Gray's Behavioral Inhibition/Activation System, the BIS/BAS Scale. The difference between their scale and Gray's original concept is that BIS and BAS are treated as independent dimensions, consistent with the view that positive and negative affect are independent, thus, individuals can be high on both, low on both, or some combination of the two. The scale, which asks participants to endorse statements like, "It would excite me to win a contest" (BAS) and "I worry about making mistakes" (BIS), concentrates on emotional reactions to positive and negative life events. The idea is that emotional reactivity to events has effects on behavior, as individuals prioritize their time and effort into achieving goals that have the biggest impact on their happiness. Thus, an individual who worries a lot about making mistakes is more likely to be cautious in situations when failure is a possibility, even in situations where the potential rewards for taking action are high.

Studies examining the BIS and BAS systems have often relied on physiological data to test claims regarding the independence of the two systems, and their relationship to individual or group differences in affective style. A key component of this work is the assumption that approach and withdrawal are associated with greater relative activity in the left or right hemispheres of the brain, respectively (for review, *see* Davidson, 2003)--for example, EEG experiments that show that depressed patients have the same level of activation in right frontal cortex as controls, and what separates them is lower left frontal activity, characteristic of low positive affect (Henriques & Davidson, 1991). Anger is an important exception because it is negative, but it is also an approach emotion that prompts individuals to act (Lerner & Keltner, 2000, 2001). In an EEG experiment dealing with motivation, Sobotka and Davidson (1992) compared conditions in which participants had to withdraw their finger quickly from a button to avoid monetary penalties or had to press a button quickly to obtain monetary reward. Right hemisphere activity was increased in the withdraw penalty condition, while left hemisphere activity increased in the approach reward condition. Further research has shown that differential activation of right and left hemispheres is a trait that underlies affective style from an early age. Specifically, children who have greater left-relative-to-right hemisphere activity at rest demonstrate a more positive affective style, while greater right than left have a more negative affective style (Fox et al., 1995). This tendency toward positive and negative style also correlated with social competence, as children with greater left frontal asymmetry displayed both more positive affect, and more socially competent behaviors in a free-play session.

Beyond emotional reactivity to events, it is possible to consider motivation as fitting into how individuals feel about themselves and their self-image. Higgins' (1999) self-discrepancy theory describes two self-guides that motivate people–the *ideal* self and the *ought* self. The ideal self possesses qualities that the individual personally aspires to, and is intrinsically motivated to attain, whereas the ought self is comprised of qualities that people feel obligated to attain. Discrepancies between the ideal self and the actual self produce disappointment and dejection, as individuals fail to achieve their personal goals. In contrast, differences between the ought self and the actual self produce anxiety, as individuals anticipate negative consequences (e.g., censure of others) for failing to achieve their obligatory goals.

The relative extent to which individuals focus on minimizing discrepancies between the actual self and these two self-guides (regulatory focus) can be measured as a stable personality trait (*see* Regulatory Focus Questionnaire, Higgins et al., 2001). Focus on the ideal versus the actual self is an indication of a promotion focus. Promotion-focused individuals direct more attention towards attaining rewards, thus they enjoy tasks that involve finding helpful items more than those that involve finding harmful items (Freitas & Higgins, 2002). Focus on the ought versus the actual self is an indication of a prevention focus. Prevention-focused individuals direct more attention towards avoiding negative outcomes, thus they enjoy tasks that involve finding (and avoiding) harmful items more than those that involve finding (and obtaining) helpful items. This concept of "regulatory fit" is one example of how personality can affect how motivated individuals are by different types of tasks.

Regulatory focus also has implications for how individuals set and pursue goals. Promotion-focused individuals tend to view goals as opportunities to achieve the best possible outcome, whereas the prevention-focused view goals as basic requirements to avoid a negative outcome. Thus, promotion-focused individuals may derive more utility from moving towards their goals than the prevention-focused. However, prevention-focused individuals tend to begin pursuit of their goals earlier (Freitas et al., 2002). Viewing a goal as a basic necessity rather than an intriguing possibility seems to urge earlier and more focused action.

Although regulatory focus can be measured as a personality trait, it can also be influenced in a state-like manner, by experimental manipulation of task conditions. Specifically, emphasizing that achievement of a goal is important to avoid negative outcomes primes a prevention focus, whereas concentrating on potential benefits primes a promotion focus. For example, participants in an experiment where the task is framed in a prevention-oriented way (write an essay in order to avoid being rejected for a fellowship and losing money) choose to begin writing the essay earlier than participants in a promotion-framed condition (write an essay to get accepted for a fellowship, and gain money) (Freitas et al., 2002).

In summary, social and personality psychology research demonstrates strong influences of a number of person and situation factors related to motivation, such as basic characteristics of affective style, and how motivational goals are framed or construed. More specifically, participants' behavior during laboratory tasks is affected by the incentives that are offered, individual differences in relative sensitivity towards reward versus punishment incentives, the types of goals set, and how progress towards those goals is monitored.

NEUROSCIENCE PERSPECTIVES

Neuroscientists have studied motivation by looking at how rewards and punishments are processed by the brain. Older views of motivation focused on "drive" models, in which the lack of an essential physiological variable is the source of drive in initiating actions to correct the deficiency. For example, a lack of food would cause foraging behavior to obtain food (Hull, 1943). The key idea was that the central nervous system implemented mechanisms for homeostasis—forces that maintain stable internal states—which correct any deviations in amount of nutrients, water, or changes in internal temperature from a set-point value. Moreover, according to the theory, drive-states also produce affective responses, with drive-reducing stimuli (e.g., presentation of a cheeseburger to a hungry person) being experienced as rewarding, and drive-increasing stimuli being experienced as aversive (e.g., presentation of salty foods when thirsty).

One of the further implications of drive theory is that stimulation that increases a behavior should be experienced as aversive, because by definition, it must have increased physiological drive. However, this inference was inconsistent with brain stimulation experiments, which showed that electrical stimulation of the same area that caused increased eating (the lateral hypothalamus) also appeared to be rewarding to the animal, as measured by tendency for the animal to also self-stimulate in that area (Valenstein, Cox, & Kakolewski, 1970). Another interesting finding from these experiments was that the response the animals gave to stimulation was not always eating—some animals drank, gnawed, or displayed sexual behavior, although which behavior was displayed was consistent within the same animal on different occasions. Thus, it seemed that the stimulation triggered a more general motivational state apart from filling (or increasing) a particular need.

In addition to providing data that conflicted with drive theory, the electrical stimulation studies also provided support for the next major theory of reinforcement, namely the idea that dopamine (DA) served as a "pleasure chemical" mediating the subjective experience of reward. In these experiments, electrical stimulation devices were implanted in limbic system structures, several in regions that are primary targets for dopamine, such as the nucleus accumbens (NAcc). These studies showed that animals and people with access to a self-stimulation apparatus often self-stimulated excessively, even to the exclusion of other motivated behaviors, including eating and sleeping (Heath, 1996; Olds, 1958). Researchers drew the conclusion that dopamine itself carried the hedonic signal, and thus by mimicking it (by directly stimulating dopamine targets), pleasurable states could be created.

However, this view was rejected by experiments in which DA was directly injected into the NAcc in conjunction with sucrose delivery (Wyvell & Berridge, 2000). In these studies, DA injection did not increase the consumption or apparent hedonic response to the sweet taste (as measured in animals by stereotypic indices of facial expression and reaction). Thus, DA did not increase liking of preferred foods (e.g., sweet tastes), which it should have if it amplified the foods' pleasure value. In addition, in studies with humans that had electrodes implanted in NAcc (for treatment of depression or debilitating pain), direct queries about their subjective experience typically yielded vague statements like, "I feel good" rather than descriptions of discrete episodes of pleasure following NAcc self-stimulation (Heath, 1996).

The hypothesis of dopamine as a pleasure chemical has been further challenged by more recent experimentation, leading to the development of several new theories of dopamine function. Below, these theories are briefly reviewed. Although they disagree with one another on the exact functional role of dopamine, they are united in rejecting the pleasure chemical hypothesis.

Modern Views of Dopamine Functions in Reward and Motivation

More recent studies of the role of dopamine in reward and motivation have relied upon direct single-cell recordings of neuronal activity within dopamine-releasing neurons in awake, behaving animals, such as primates. A key finding of this work is that dopamine neurons show phasic activity in response to reward-related information at the time of delivery for unpredicted rewards. Yet when rewards are predictable the dopamine response occurs to earlier reward-predictive cues and not to reward delivery itself (Schultz, 2002). These findings suggest that the dopamine system does not convey the hedonic aspects of reward, but rather acts as an informational signal about whether and when rewards will be delivered. This type of reward-prediction or reward-learning system could help to strengthen perceptual and response pathways that help maximize the obtainment of reward.

The theory of dopamine as central to reward learning has been challenged by experiments with animals where ascending DA pathways were nearly completely destroyed. Despite not having dopamine, these animals were able to learn an aversive reaction to a previously liked sweet taste when the sweet taste was paired with LiCl, a chemical that causes gastric distress (Berridge & Robinson, 1998). Later experiments showed that dopamine deficient mutant mice were able to learn the location of a food reward when given caffeine, but that the learning was not revealed until the mice were treated with L-DOPA, a DA precursor (Robinson, Sandstrom, Denenberg, & Palmiter, 2005). Together these results suggest that DA is not necessary to learn hedonic and behavioral responses to reward-related stimuli. Yet at the same time, the latter result provokes questions about why behaviors required to acquire reward are impaired in the absence of DA.

Berridge and colleagues, who emphasize that DA serves a motivational rather than hedonic function in the processing of reward, have put forth a response to this puzzle. Specifically, Berridge's view is that above and beyond informational aspects of reward (what is it? where is it?), and the hedonic or "liking" aspects of a reward, the system must produce a motivational state to induce a change in behavior (Berridge & Robinson, 1998). Berridge and Robinson attribute reward "wanting" or incentive salience to the action of the nucleus accumbens, which they suggest is the brain structure responsible for translating pure factual information about an available reward into a more affective desire to have it. This step could then feasibly lead to changes in behavior necessary to obtain the reward.

Support for the role of NAcc in wanting rather than liking has come from experiments demonstrating a clear dissociation of DA manipulations on hedonic responses vs. goal-directed instrumental behavior. Specifically, as described above, NAcc DA depletion in rats has no effect on sucrose consumption or facial displays of liking, but does dramatically decrease behavioral responses (e.g., lever pressing or maze running) required to obtain the reward (Berridge & Robinson, 1998). Moreover, Berridge suggests a reinterpretation of the NAcc self-stimulation studies, arguing that animals and humans are driven to self-stimulate in these situations because DA release can increase incentive salience in a general way, leading the world to look like a more attractive place (i.e., full of more valued rewards) rather than directly inducing a hedonic "pleasure" response (Berridge & Robinson, 1998).

Berridge is very clear in dissociating incentive salience "wanting" from the colloquial use of wanting, "cognitive wanting" (Berridge, 2004). Whereas incentive salience is not necessarily conscious, cognitive wanting is a declarative representation of a goal, based on previous experience with it, or an internal estimation of its value. In cognitive wanting, an understanding of the causal relationship between an individual's actions and the likelihood of obtaining the reward is necessary to facilitate those actions that lead to reward obtainment. In other words, a decision to pursue a reward is based on an expectation of how much the reward will be liked. Incentive salience, by contrast, can be triggered by mere perception of a stimulus, and can lead to irrational wanting of something that is not expected to be liked, such as a drug of abuse (Berridge, 2004).

The incentive salience model of addiction states that drugs that cause DA release create a false association of that drug (or drug paraphernalia) with an abnormally high "wanting" even when the drug user is long past the point when the drug use is actively enjoyed. Thus, drug users desperately "want" something they do not "like." This effect is especially pernicious because of how long it lasts. Whereas tolerance effects (fewer DA receptors as a result of repeated overabundance of DA in the synapse) disappear in a matter of weeks, sensitization effects can last for years, leading to a risk of relapse when encountering drug-related stimuli (Robinson & Berridge, 2000).

Thus, according to Berridge, motivation is not a drive-reducing process that attempts to correct deficits in reward signaled by the level of DA release. Instead, it is a process by which incentive salience becomes attached to stimuli, such that these stimuli attract approach-related behaviors that vary in strength in proportion to the estimated magnitude of salience. In contrast, the experience of actual liking, in Berridge's view, is mediated by an opiate system in the NAcc shell. This view is supported by findings that injection of opiates there increases positive taste reactions to sweet foods and promotes eating, while opiate blockers decrease positive taste reaction and decrease eating (Peciña & Berridge, 2000). Nevertheless, it is important to note that in a normally functioning system, wanting and liking of rewards go together, such that appropriate actions are implemented to gain a liked reward.

Panksepp has a similar view of DA function, in that it is primarily involved in instrumental behaviors needed to obtain rewards, rather than subserving the pleasure or liking of the reward itself. But unlike Berridge, Panksepp's view is not that NAcc mediates wanting, but rather "flexible seeking behavior" (Ikemoto & Panksepp, 1999). Thus, contrary to what would be predicted by the incentive salience hypothesis, when comparing two groups of hungry rats in a novel environment, the group that is dopamine-depleted will actually eat more than the control group (Koob et al., 1978). Panksepp explains these results by characterizing DA as a driver of exploration, and reward seeking. Thus, for normal rats in a novel environment, exploratory behaviors will be facilitated even at the expense of eating. In contrast, dopamine deficient rats feel no compulsion to explore and instead just eat their fill. Further, recordings of dopamine levels in the nucleus accumbens show that DA is especially high in thwarting paradigms, such as when a male rat is prevented from accessing a female rat. In these situations, the reward value of the female rat should be constant, but what is maximized is seeking behavior, as the test rat tries a large variety of behaviors in order to get to the female.

Another important distinction between Berridge and Panksepp is that Berridge does not distinguish between dopamine effects in the nucleus accumbens and dopamine in the dorsal striatum (i.e., the caudate and putamen structures of the basal ganglia), whereas Panksepp sees the two as very different. In Panksepp's model, dopamine projections from the ventral tegmental area (VTA) to the NAcc underlie flexible seeking behaviors, whereas dopamine projections from the substantia nigra to dorsal striatum mediate already learned behaviors (habits). Thus, when animals have already learned self-administration of a drug like heroine, or ethanol, selective dopamine depletion in the NAcc does not disrupt this behavior. Rather, because the drug use has become a habit, the nigro-striatal pathway is able to maintain the behavior. This is in contrast to the incentive salience hypothesis, which should predict that self-administration would be affected by the inability to attach salience to drug-related stimuli, and initiate approach.

Another closely related idea about dopamine's function has been advanced by Salamone (Salamone & Correa, 2002). Like Berridge and Panksepp, Salamone rejects the theory of dopamine as pleasure chemical, and instead believes DA has a central role in motivation. Further, he takes Berridge's concept of "wanting" and deconstructs it into two distinct aspects: directional (desire for a specific reward) and activational (willingness to initiate goal-directed behavior towards obtaining a reward). In Salamone's view, dopamine is critical for the activational aspect of wanting, but does not influence the appetitive value of rewards. He cites as evidence a number of studies in which dopamine antagonists impair instrumental responses for reward (e.g., lever pressing) but do not disrupt reward choice, or simple approach and consumption of food rewards.

Indeed, several studies cited by Salamone (e.g., Caul & Brindle, 2001) demonstrate that even fairly high doses of a DA antagonist like haloperidol will not disrupt performance on reward tasks that are not demanding. Thus, the appetite for the reward is not diminished, but rather the willingness to work for the reward. What DA reduction does, then, is alter the balance between costs and payoff, such that the costs seem to loom larger, making the animal less likely to put forth the effort to get the reward.

The role of dopamine in reward processing remains controversial, with researchers arguing for reward learning (Schultz), incentive salience (Berridge), flexible seeking (Panksepp), reward-directed action (Salamone), as well as other hypotheses. Nevertheless, there does seem to be a basic agreement that dopamine is intimately involved in motivation. For a normal response to new rewards in the environment to be accomplished, dopamine transmission is essential. However, what the animal or person does with reward information to change behavior is also critical if rewards are to be obtained rather than merely discovered or coveted.

Neural Circuitry of Reward Motivation

Dopamine neurons project to number of brain regions, not only to the ventral (NAcc) and dorsal (caudate and putamen) components of the basal ganglia, but also to medial and lateral frontal cortical regions. These projection sites appear to be involved with further processing of reward-related information. For example, it has been theorized that the basal ganglia is a site where rewards are linked to goal-directed motor actions (Kawagoe et al., 1998). Experiments in macaques recording the activity of neurons in the caudate during a saccade task have shown that introducing rewards can radically alter their activity (i.e. firing rates). At baseline, caudate neurons are selectively sensitive to stimuli in a particular location, usually the contralateral half of the visual field. However, when rewards were associated with only the nonpreferred direction, these neurons changed their preference, and responded more vigorously to the rewarded direction. This switch in preference was associated with faster and more accurate saccade responses to the rewarded direction (Kawagoe et al., 1998).

Reward signaling has also been investigated in humans, where several studies have used gambling-type tasks with differential reward payoffs to identify the basic neural circuitry involved in signaling reward. For example, Delgado et al. (2000, 2003) used such a paradigm, in which participants were asked to guess whether the value of a face-down card was higher or lower than five, with monetary rewards provided for correct guesses. Imaging results showed that in the caudate nucleus, a sustained hemodynamic response was observed on reward trials, whereas penalty trials led to a sharp drop-off in activation, with the basic valence effect also showing scaling according to the magnitude of the reward or punishment. This reward signaling is potentially useful for flagging certain actions or decisions as being associated with a positive outcome.

Reward representation refers to maintaining information about the type and current value of a reward (which may be context dependent), as opposed to merely signaling the presence or absence of a reward and/or its magnitude. Studies of reward representation have suggested the importance of areas within prefrontal cortex (PFC), specifically orbitofrontal cortex (OFC), for this function. A basic requirement of reward representation is being able to represent valence distinctions, as also occurs within basal ganglia structures. Consistent with this assumption, OFC regions appear to be anatomically dissociable in regards to valence effects. O'Doherty et al. (2001) found that medial areas of OFC activated to reward, whereas lateral areas responded to punishment during a reversal learning task with monetary reinforcers. Since this original finding, this basic pattern of spatial dissociation has been replicated a number of times (Kringelbach & Rolls, 2004).

Brain regions that represent reward value need to be able to integrate different categories of reinforcement into a unified representation of value (Montague & Berns, 2002; Montague & Cohen, 2006). Thus, when faced with a choice between rewards that are hard to compare, for example, an ice cream cone vs. an hour of reading a good book, individuals are able to consider their internal state (hunger, fatigue), general preferences for those activities, costs of the two options, and so forth, and generate a value for each. Representing the value of rewards in a way that would make them directly comparable would allow resources to be directed toward achieving the most attractive reward. The OFC appears well positioned for this function, as it shows responses to stimuli that appear to code them in terms of both their hedonic properties, which might be context-dependent, and their value to the individual in relationship to other potential reward-related stimuli.

These two properties of OFC function can be seen in terms of its response to primary sensory reinforcers, such as taste and smell. The role of the OFC in these domains is well established, given its strong anatomical linkage to primary gustatory and olfactory cortex (Rolls, 2001). Indeed, caudolateral OFC has been termed the secondary taste cortex (Rolls, 2001). In contrast to primary taste cortex, which responds consistently to taste sensation, secondary taste cortex ceases responding to tastes when the animal has been fed to satiety. Thus, Rolls (2005) states that secondary taste cortex represents the reward value of taste. However, as with abstract rewards, there is evidence that both positive and negative stimuli are represented in the OFC, as in O'Doherty et al. (2001), where positive taste (glucose) and negative (saltwater) were found to activate different parts of secondary taste cortex. The OFC response is also strongly sensitive to the organism's stable reward preferences. In free choice situations, OFC shows greater activity for the most preferred reward (Tremblay & Schultz, 1999). More recently, it has been shown that reward value in terms of choice preference appears to be directly coded in the level of activity within single OFC neurons (Padoa-Schioppa & Assad, 2006). In humans, a food stimulus once considered rewarding may also be represented as punishment if the individual is over-satiated (Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001). This result was replicated using liquids (tomato juice and chocolate milk) contrasted with a flavorless solution approximating saliva. The liquids which were ingested to satiety failed to activate OFC, whereas the liquid which was not continued to activate OFC (Kringelbach et al., 2003).

Although the primary focus on the prefrontal cortex with regard to reward-related processing has been on the OFC, some studies have revealed activation in the lateral prefrontal cortex (LPFC) as well. For example, Leon and Shadlen (1999) investigated reward incentive effects during cognitive task performance within area 46 in macaques, a region analogous to the human dorsolateral PFC. The traditionally assumed function of this region is to maintain goal-related information in working memory over short delays. Neurons in area 46 respond maximally to stimuli in a specific part of the visual field, maintaining this position over a delay so the animal can remember the location of a stimulus after is has disappeared. They found that the stimulus-specific neuronal activity was enhanced when an incentive cue indicated the possibility of a large reward for correct performance. This increased activity may have been indicative of a stronger representation of the location of the stimulus, which would have been advantageous in performing the task.

Watanabe et al. (2002) contend that the LPFC may in fact be a site of integration of cognitive and motivational operations that contribute to goal-directed behavior. Using single-cell recording in monkeys during a go/no-go task, they found a subset of neurons that discriminated between rewarded and unrewarded trials. Specifically, they increased firing in reward trials compared to unrewarded trials during the delay phase of the task. Higher activity was associated with more preferred rewards such as cabbage. The authors also looked at baseline activity and found significant differences, such that tonic activity levels were highest during blocks of trials in which the preferred reward was available (highest for cabbage). They theorize that this baseline activity in the different blocks may reflect continuous monitoring of the motivational context, and may be an index of motivational level. Regarding anatomy, the authors suggest a dorsal/ventral split, with dorsal activity reflecting the continuous monitoring of motivational context, and the ventral and arcuate areas tracking the motivational value of the presence or absence of individual rewards.

Although the precise functions of the dopamine system, the nucleus accumbens, the caudate nucleus, and the OFC are still under investigation, there is general agreement that these regions make up a reward processing system that handles reward information. In summary, when a reward is available in the environment, an animal must make a series of judgments about how intrinsically attractive is that reward, its relative value, which is dependent upon both stable preferences and transient fluctuations in internal state, and how much it costs to obtain the reward, in terms of required effort. If the reward is deemed worth the effort required, instrumental actions must be initiated to get the reward.

Neural Circuitry of Punishment Motivation

A great deal of research has been conducted to understand the neural circuitry of rewards and their relationship to instrumental behavior. Less is understood about how animals and humans process punishments or other aversive outcomes. One possibility is that punishments are coded within the same dopaminergic system as rewards. For example, Panksepp has commented that his theory of nucleus accumbens dopamine function, in which dopamine facilitates flexible approach toward rewards, can be equally applied to punishment, in that avoiding an aversive outcome entails approach toward safety, an incentive (Ikemoto & Panksepp, 1999). In Schultz's theory of reward learning, he notes that missed rewards depress dopamine firing, but given that DA cells have a resting firing rate of around five action potentials per second, there is not a large range to decrease to incorporate negative events (rather than just the absence of positive events) (Grace & Bunney, 1984). Indeed, Mirenowicz and Schultz (1996) showed that aversive stimuli closely matched to appetitive stimuli (saltwater and juice, respectively, that were calibrated to prompt the same behavioral performance) failed to activate dopamine neurons. Given this limitation, some researchers have proposed that incentive processing is a rectified system, whereby positive and negative incentives are processed by separate neural mechanisms.

The leading candidate for a neural counterpart mechanism to dopamine, in conveying punishment-related incentive signals, is the serotonin system. Serotonin (5-HT) projects widely throughout the nervous system, and has a myriad of functions (for a review of serotonin and behavior, *see* Lucki, 1998). The dorsal and medial raphe nuclei in the midbrain are the source of the serotonin that projects to the forebrain. One particular pathway that has received attention in motivation research is the projection of serotonergic cells from the dorsal raphe to the ventral striatum, also a target of dopamine cells. Due to this association, researchers (e.g., Daw et al., 2002; Deakin, 1983) hypothesized that serotonin and dopamine are opponent systems. Whereas dopamine facilitates approach behaviors towards positive stimuli, serotonin inhibits these behaviors, and mediates avoidance in the presence of aversive stimuli. Depending on which influence was stronger, the net result would be either approach or withdrawal. Daw et al. (2002) in particular extend the reward learning model of dopamine function to suggest that serotonin neurons' activity signals an error in the prediction of punishment, just as DA neurons signal an error in the prediction of reward.

In addition to questions regarding whether there is a distinct signaling mechanism that conveys information about punishments and aversive outcomes, it is also of interest to determine whether there are independent neural circuits for further processing this information, or if the neural circuitry of punishment overlaps with that for reward. There is some evidence for distinct components within the neural circuitry of punishment, such as the anterior insula and amygdala (Seymour et al., 2007). In animals, activity in the basolateral and central nuclei of the amygdala, respectively, has been associated with learning to predict and avoid aversive outcomes, such as an air puff to the face (Everitt et al., 2003; Paton et al., 2006). In humans, research has shown that amygdala damage is associated with the inability to learn associations between visual stimuli and negative outcomes such as a loud noise (Bechara et al., 1999), or an electric shock (LaBar et al., 1995). Insula activity has been observed in neuro-imaging paradigms that involve emotionally unpleasant (e.g., Coan et al., 2006), disgusting (e.g., Calder et al., 2007), or unfair outcomes (Sanfey et al., 2003).

In addition to its potentially unique components, the neural circuitry of punishment also appears to partially overlap with reward circuitry, since both seem to involve basal ganglia structures. For example, as discussed above, many investigators suggest that the nucleus accumbens plays a bivalent role in motivation, responding to both rewarding and aversive events (Salamone, 1994). Similarly, human neuro-imaging studies have observed nucleus accumbens direct activation during anticipation of not only rewarding but also aversive outcomes (Jensen et al., 2003). Nevertheless, some evidence suggests those positive and negative valences are represented in distinct anatomical subregions within the nucleus accumbens (Reynolds & Berridge, 2002).

The prefrontal cortex also appears to play a common role in processing both reward and punishment information. Single-cell recording experiments in primate LPFC, similar to those previously discussed examining effects of reward, have contrasted the effects of rewarding and aversive stimuli (Kobayashi et al., 2006). The goal of these studies has been to determine whether LPFC neurons also respond to punishments, such as an air puff to the eye, as potential outcomes for poor performance in tasks. Monkeys were to remember the location of a target over a 1- or 2-second delay, and then saccade to its location, which was the same task performed in the Leon and Shadlen (1999) study. Results showed that although the majority of neurons were sensitive to rewards only, a smaller, separate group was found that responded preferentially to punishments. Specifically, these neurons significantly increased or decreased their rate of responding during the delay period after cues indicating the possibility of an air puff. Unlike Leon and Shadlen (1999), they did not manipulate incentive magnitude, and thus it is not known whether larger punishments would be associated with greater changes in firing rate.

Roesch and Olson (2004) used a similar task, except that both reward and penalty were possible on each trial. Additionally, they focused on the OFC as well as a posterior region of LPFC (the premotor cortex). Each trial featured two locations, one of which displayed a cue indicating that a reward would be available if the monkey performed a saccade to that location, and the other indicating that a penalty would result if the monkey moved its eyes to that location. Punishments in this task were time-outs of 1 to 8 seconds, an aversive outcome because the thirsty monkeys were unable to perform trials to get liquid rewards during this time. Results showed a dissociation in the activity between OFC and premotor cortex. OFC neurons responded to the overall value of the cues present on each trial (i.e., the value of the reward minus the value of the punishment), whereas premotor cortex responded vigorously to both types of incentive relative to the neutral condition. Premotor neurons responded maximally to the high-reward, and high-penalty conditions. The authors suggest that these results stem from a distinction of the function of these two areas, such that OFC represents the combined value of potential incentives, whereas the premotor cortex represents the motivational impact of the incentives (i.e., that there is something of value at stake, whether positive or negative). However, it is still possible that distinct OFC subregions code for negative and positive value, as appears to occur within other structures such as the nucleus accumbens. Human neuroimaging studies provide evidence consistent with this type of organizational structure, with rewarding stimuli activating medial OFC, and aversive stimuli activating lateral OFC regions (O'Doherty et al., 2001).

Human neuroimaging studies examining the motivational effects of punishments are still sparse (partly because of increased ethical concerns), but a few imaging studies have been conducted during cognitive task performance. Small et al. (2005) conducted a spatial attention task using both positive and negative monetary incentives. In a replication of a previous study, they found that the amount of spatial biasing (directing attention to a cued location to be faster when the target appears) was correlated with activity in the posterior cingulate cortex (Small et al., 2003). Further, activity in PCC was enhanced by both positive and negative incentives, but the effects these had may have been mediated by separate limbic structures. The possibility of winning was associated with activity in OFC, while losing activated dorsal anterior cingulate cortex and insula. Small et al. (2005) make the point that all three of these regions are connected with PCC in the macaque, and if this is also the case in humans, they may mediate the increased activity in PCC they observed. Given the connectivity of PCC with limbic structures and its association with direction of attention, Small et al. (2005) have proposed that posterior cingulate cortex is a site of integration of motivation and top-down attentional control.

Taylor et al. (2006) manipulated whether errors produced monetary penalties or not during performance of an Eriksen flanker task. They also observed that potential for penalty led to increased activity in the ACC but in a rostral rather than dorsal region. Because there was no matched reward condition in this study, it was not possible to determine whether the effect in ACC was valence-selective.

In summary, neuroscience experiments have mapped out a network of brain regions that signal reward and punishment in the environment and represent those incentives such that they could be used as information to guide action choices and effort levels. However, this careful body of work has less to say about what happens to that information, and how it is integrated into ongoing processing that directly affects behavior.

COGNITIVE NEUROSCIENCE PERSPECTIVES

Both top-down social/personality theories and bottom-up neurobiological theories of motivation contribute to a greater understanding of motivation. Social and personality researchers focus on how the goals and attributions of individuals, as well as the social context, influence motivation to engage in particular tasks. Additionally, there is a strong emphasis on individual differences, such as the role of reward and punishment sensitivity as stable trait characteristics. Neuroscience-based theories focus on the neural systems responsible for generating a desire for rewards and translating this into simple instrumental actions like lever pressing to obtain rewards. The gap between these two is a process-level account of how people are able to channel their motivation to gain desired rewards into improved performance in more complex behavioral tasks. Cognitive neuroscience approaches may fill this gap by illuminating the neural mechanisms that translate wanting into getting. Specifically, cognitive neuroscience studies involve directly examining human brain activity during performance of cognitive tasks. Motivation can be studied in this context by examining how task-related brain activity is affected both by changes in motivational state (i.e., experimental manipulations), and motivation-related individual differences. Two possibilities are: *(1)* effects on high-level cognitive control structures and *(2)* direct effects on activity in task-related regions.

Cognitive Control Processes in the Brain

In any cognitive task, there are brain regions that make their contribution not by facilitating task-specific components of processing, but rather in the higher-level coordination and regulation of task elements. These processes of high-level coordination and regulation are collectively referred to as cognitive control functions. Cognitive control refers to the process by which cognition and behavior is directed towards the fulfillment of internally generated goals (Miller & Cohen, 2001). Many of the processes by which control is exerted during tasks, including sustained attention, task set maintenance and task preparation, and interference prevention, have been localized to the prefrontal cortex, particularly lateral prefrontal cortex. Miller and Cohen (2001) argue that the central theme to these functions is that the prefrontal cortex is able maintain information about goals, and how to achieve them, in a manner that is less susceptible to interference.

Motivational incentives may enable improved performance by influencing cognitive control functions. Specifically, task performance may improve with tighter control over cognitive processing and monitoring of behavioral performance, such that negative events like interference or momentary lapses of attention are prevented. Similarly, errors will be less frequent when participants successfully maintain task instructions in a highly accessible form that ensures maintenance of attentional focus and suppression of interference from distracting events. These operations are potentially costly, in terms of subjective mental effort and metabolic demands, but the possibility of reward may shift the cost–benefit relationship, leading to increased activity in cognitive control structures that enhance performance.

Locke and Braver (2008) looked at the effects of motivational incentives on brain activity in a continuous performance task (AX-CPT) that serves as a probe of cognitive control function. In previous neuroimaging studies of the AX-CPT, task performance is reliably associated with increases in lateral PFC activity associated with the active maintenance of task-relevant goals (Miller & Cohen, 2001). Locke and Braver (2008) found that under reward incentive conditions (good performance was associated with monetary bonuses), there was a sustained increase in activity within brain regions associated with cognitive control function. These included right lateral PFC, right parietal cortex, right inferior frontal cortex (BA 45), and left dorsal anterior cingulate (BA 32).

Right lateral prefrontal cortex (RLPFC) and right parietal cortex are thought to be the core components of a brain network that mediates sustained attention (Pardo et al., 1991; Posner & Petersen, 1990). Right inferior frontal cortex (RIFC) has been implicated in cognitive inhibition, or the suppression of irrelevant thoughts, memories, or responses (Aron, Robbins, & Poldrack, 2004). And finally, anterior cingulate activity, particularly dorsal anterior cingulate, has been implicated in the detection and resolution of response interference or conflict. Together, the increased tonic activity in these regions may reflect the greater level of cognitive control exerted by participants in the reward-incentive condition in order to improve performance and maximize reward attainment.

A theory of how individuals increase cognitive control processes to maintain or improve performance has been described in a review of the neurobiology of attention (Sarter et al., 2006). In response to theories of attention that focus solely on task demands, the authors counter that motivation to maintain attention is key, particularly in situations where there is a challenge, such as a distracter, a dual task, or general fatigue. In this theory, a decline in performance or increased response conflict is detected by the anterior cingulate, which then can call for increased attentional effort, depending on the costs and benefits of continuing versus disengaging. A right-lateralized frontoparietal network, the anterior attention network, can then exert top-down influences via cholinergic projections to sensory systems to reduce processing of distracters.

Pochon et al. (2002) demonstrated an increase in activity in regions associated with executive control in humans in an fMRI study. Comparing activity in an N-back task when reward was offered relative to activity when no reward was offered yielded an increase in activity in dorsolateral prefrontal cortex (DLPFC), an area involved in maintaining a task set. In their study, both increases in task demand and reward increased activity in DLPFC. A similar pattern of findings was observed in Taylor et al. (2004). These studies suggest that reward may act as a kind of call for increased effort in a similar way as a change in actual task demands. In both instances, more effort is required to maintain or improve behavior.

Interestingly, Pochon et al. (2002) also reported the recruitment of lateral frontopolar regions in response to reward. Frontopolar cortex is a region that has been hypothesized to be involved in goal–subgoal coordination, that is, maintaining an overarching goal while simultaneously performing a task with its own local set of subgoals (Braver & Bongiolatti, 2002; Koechlin, 1999). According to Pochon et al. (2002), reward, or what is at stake at any given moment, may be represented in the form of a primary, high-order goal in the frontopolar region. This goal may then coordinate the processing and management of subgoals that enable optimal completion of the task.

Gilbert and Fiez (2004) aimed to investigate the integration of reward and task in lateral PFC during working memory performance. They predicted that ventral PFC would show cue-related responses only when these indicated the potential for reward. Instead, the results indicated that following reward cues there was a significant decrease in ventral PFC activation during the delay period, while DLPFC activity increased. They attributed this result to an oppositional relationship between emotional/motivation regions and cognitive regions, such that a decrease in the former is necessary to obtain optimal performance in the latter (Gilbert & Fiez, 2004).

Task-Relevant Activity in the Brain

The second pathway for reward to have an impact on task performance would be through reward acting on the existing architecture that supports task-specific processing. When comparing regions that would normally be used to do a task under no-incentive versus incentive conditions, it may be possible to see enhanced activity in specific task-related brain regions, as a key means of improving performance. For example, Taylor et al. (2004) demonstrated an increase in activation in task-relevant regions in an object working memory study. In their study, they were able to decompose the trials into discrete phases, and during the delay phase they found increased activity in the premotor superior frontal sulcus and the intraparietal sulcus. These areas, involved in short-term storage of visuospatial information, also increased in response to working memory load. This suggests, as in Pochon et al. (2002), reward may elicit enhanced processing in a similar manner as an increase in task demands.

Although Pochon et al. (2002) showed prefrontal regions operating in a cognitive control capacity, such regions also project to task-relevant areas. Visual attention, for example, the way objects are selected for attention from an array of competing objects, may depend on a top-down biasing signal from PFC (Desimone & Duncan, 1995). During tasks with visual stimuli, it may be possible to see increased activity in visual processing areas as a result of top-down influences from prefrontal cortex. This may aid individuals in focusing attention on stimulus objects, or their particularly relevant features.

Even without reward incentives, participants may selectively enhance task-specific processing regions in accordance with task demands. An example of such a situation can be seen in the classic PET study of Corbetta et al. (1991), in which participants were asked to alternate attentional focus to specific stimulus dimensions (e.g., color, motion, shape) during a same–different matching task. Each dimension was associated with increased activity in the corresponding relevant regions of extrastriate cortex (e.g., attention to motion was associated with increase in area MT). In contrast, when participants divided their attention across a number of different features, activity was not greater than in extrastriate cortex compared to a passive viewing condition. Each of the selective attention conditions were also associated with activity in attentional regions such as the pulvinar, a finding the authors attribute to its role in directing visual attention.

In the study by Small et al. (2005), discussed above, that used rewards and punishments during a spatial attention task, the authors suggest that incentives modulated structures directly involved with spatial representation. Specifically, the posterior cingulate cortex, a region that had previously been observed to show correlations between activation level and degree of spatial biasing (increased speed of target detection when previously spatially cued to the relevant location), also showed further modulation by incentives. Small et al. (2005) hypothesized that posterior cingulate cortex is a site of integration of motivation and spatial attention control.

A study by Krawczyk et al. (2007) investigated activity related to perception of scenes (parahippocampus activity), and perception of faces (fusiform gyrus activity). Trials presented both scenes and faces, with participants instructed to attend to one category and ignore the other. Results showed that activity in the relevant region increased for the attended category, and decreased for the ignored category, relative to a passive viewing condition. These effects were magnified by the opportunity to earn points that could be exchanged for money. Together, these results suggest that attention can enhance activity in perceptual regions relevant to a given task, and that reward can amplify these attentional effects.

Effects of Individual Differences

The majority of studies in cognitive neuroscience focus on what is common across individuals. A cognitive process under study is investigated by running a number of participants and taking a group average. The key interest is in identifying variance that can be explained by the experimental manipulations, whereas differences among the participants are treated as error variance (Thompson-Schill et al., 2005). This approach works well in identifying regions associated with a core set of functions necessary for a task, because presumably these regions will be the same for every participant as they perform the task. What may be missing is activity in regions that aren't necessary but are optional resources individuals may bring to bear to perform well at a task. This kind of activity may be particularly relevant to motivation, as increases in motivation should be associated with greater use of resources to acquire rewards or avoid punishments. The use of individual differences measures, therefore, may be useful in identifying such regions (Locke & Braver, 2008).

Studies of how stable personality traits modulate brain activity are still in their infancy. Nevertheless, this work has already begun to reveal that motivation-related individual differences may influence how cognitive tasks are performed. Several studies have focused on the relationship between BAS and brain activation, mostly using EEG methods (e.g., Sutton & Davidson, 1997). More recently, fMRI studies of working memory and cognitive control have examined how task-related activity may be modulated by individual differences in BAS. Gray and Braver (2002) demonstrated that BAS scores were related to activity in the ACC during a working memory task. Specifically, higher BAS scores were associated with decreased activity in the caudal "cognitive" ACC, despite no differences in performance between high and low BAS participants. A follow-up study (Gray et al., 2005) indicated that this same pattern described a number of components of the cognitive control network (e.g., lateral PFC, parietal cortex). Moreover, a multiple regression analysis indicated that the effects of BAS on cognitive control-related brain activity were independent of individual differences in fluid intelligence (which also showed separate modulatory effects on activation). This suggests that BAS is associated with greater cognitive efficiency. Greater efficiency in cognitive control structures could be potentially useful in complex tasks like social interaction, which more extraverted individuals excel at, and which require the ability to multitask (Lieberman & Rosenthal, 2001).

Effects of BAS have also been found on brain activity during more motivationally relevant tasks. Beaver et al. (2006) monitored brain activity while participants looked at pictures of appetizing food (contrasted with bland foods). They found BAS correlated with activity in a network of reward-sensitive regions, including ventral striatum, amygdala, and orbitofrontal cortex. Specifically, activity in these areas was correlated with the BAS drive scale, which measures the motivational, as opposed to seeking or hedonic aspects of reward. The BAS drive scale includes statements like, "When I want something I usually go all-out to get it." The authors argue that this subscale is especially sensitive because it most closely related to motivation per se, the drive to attain rewards in the environment, rather than to seek out new opportunities (fun-seeking), or the tendency to react strongly to receipt of rewards (reward sensitivity).

Other personality dimensions may also be relevant to motivation and reward processing. Pailing and Segalowitz (2004) examined how motivation and personality influenced behavioral performance and the neural response to error commission. Previous research on error detection and the anterior cingulate had shown that a specific brain wave form, the error-related negativity or ERN, could be observed following errors on a task. Pailing & Segalowitz found that although performance did not significantly differ in the different motivation conditions, the magnitude of the ERN was associated with the amount of reward available, such that making a mistake on a trial where a larger reward could have been achieved was associated with a larger ERN. ERN magnitude was also associated with scores on personality measures such as the conscientiousness subscale of the IPIP-NEO. As conscientiousness scores increased, differences in ERN amplitude across conditions decreased, perhaps because highly conscientious participants were equally concerned about making errors in all conditions. Conversely, Luu, Collins, and Tucker (2000) found that ERN amplitude was negatively correlated with trait differences in negative affect (NA), such that high NA individuals showed smaller ERNs. Interestingly, the effect interacted with time on task, such that high NA individuals initially showed greater amplitude ERN responses in the first task block, but in later task blocks showed a significantly decreased ERN response. The authors interpreted this pattern as suggesting that experience with a high degree of errors (which were induced by task demands and a quick response deadline) led the high NA individuals to eventually disengage from the task, in terms of attentional effort expended.

Differences in promotion and prevention regulatory focus were the subject of an fMRI study looking for neural correlates of these personality characteristics. In the study, participants made good/bad judgments about words while in the scanner. Results were that participants showed greater activity in amygdala, anterior cingulate, and extrastriate cortex to stimuli that were congruent with their regulatory focus, positive stimuli for the promotion focused, negative stimuli for the prevention focused. These results are consistent with the idea that regulatory focus influences how attention is allocated to incoming stimuli, such that more motivationally relevant stimuli garner more attention (Cunningham, Raye, & Johnson, 2005).

The studies outlined above show that some of the trait differences in personality have provided explanatory power in recent neuroscience studies using neuroimaging and EEG methods. They suggest that it may be possible, as well as desirable, to include measures that assess motivation-related concepts and traits in neuroscience experiments, particularly those that provide incentives for performance.

In summary, cognitive neuroscience experiments have provided evidence of how the presence of rewards and punishments in the environment may influence cognitive control and task-relevant regions of the brain to facilitate performance. By marshalling cognitive control processes to sustain attention, and maintain goals while suppressing interference, individuals can focus on the task at hand. By increasing activity in task-related regions, individuals can enhance detection and maintenance of relevant information, which can lead to faster and more accurate execution of responses. As demonstrated in classic experiments like Corbetta et al. (1991), since replicated a number of times, these processes can be engaged in response to tasks without any incentives. However, the recent research in motivation and the brain shows that incentives may engage these systems to a greater extent, as individuals attempt to maximize rewards (and/or minimize punishments) by doing well at a task. Finally, the engagement of at least a subset of the neural circuitry modulated by reward (and punishment) appears to be scaled further by stable individual variation in motivationally-relevant personality traits.

CONVERGENCE IN MOTIVATION RESEARCH

The previous sections have outlined the views of different groups of researchers working on motivation-related questions from different perspectives. Social and personality research has focused on how the framing and prioritization of goals, along with personality differences, influence the motivational structure of a situation. Neuroscience research has focused on theories that describe how the brain processes rewards and punishments. Cognitive neuroscience research has begun to show how both reward and punishment information, and motivation-related individual differences, can interact with regions in the brain responsible for cognitive control and task processing. Given the diverse methodologies and theoretical frameworks of these areas of research, drawing connections between them can seem like a daunting task. However, in studying motivation from multiple angles, it appears that there may be some convergence in the lines of research in what they reveal about motivation.

The hallmark of motivation is that it directs action toward a goal, whether intrinsically generated, or externally imposed. In the cognitive neuroscience literature, research indicates that areas of lateral prefrontal cortex are responsible for maintaining goals, and biasing ongoing processing towards the furtherance of goals. Deviations from goal pursuit are inhibited, and regions like anterior cingulate detect conflict to call for more control if needed. This process relates to Carver et al.'s (2000) feedback loop model of motivation in that a goal value is set, and progress towards that goal is closely monitored. However, what Carver et al. (2000) add to the standard cognitive model is that progress or lack thereof leads to positive or negative affect, respectively. It may be possible to incorporate affect into cognitive control in a region like anterior cingulate, which has both cognitive and affective functions, thus serving as a potential convergence zone.

Taylor et al. (2006) proposed a similar idea, namely that rostral ACC activity is reflective of the affective significance of monetary loss. It is possible to imagine that setbacks in progress towards the goal may have cognitive consequences (call for more top-down control) as well as affective consequences (negative feelings associated with setbacks). Similarly, Small et al. (2005) have looked at posterior cingulate cortex, and in noting that it is active in top-down control of attention, but also has rich connections to affective and motivational regions such as orbitofrontal cortex, have proposed that it may have a role in integrating emotion and attention.

The concept of the active self (Baumeister et al., 1998, 2000), which is responsible for inhibiting habitual responses or actions that may be tempting but are contextually inappropriate, bears more than passing resemblance to cognitive psychologists' view of inhibitory control. Importantly, however, in the active self literature, engaging this inhibitory mechanism for even very short amounts of time can have devastating effects on behavior by reducing the resources available for other physically or cognitively effortful tasks. This same dynamic does not appear to be present during cognitive situations involving inhibition. Performance can be maintained in typical cognitive inhibition tasks like the Stroop or a go/no-go across hundreds of trials.

The discrepancy between active self and cognitive inhibition paradigms may be that in the former, but not the latter, participants' persistence at a task is the relevant dependent variable. In this type of scenario, the choice may really be between staying in the laboratory versus leaving to do any number of other things. In certain situations there are conflicts between goals. In a laboratory setting, a participant might have the intention to do well on a task, but he or she also might want to leave early and get a cup of coffee. There may be something special about conflicts that pit two motivationally relevant choices against one another. This type of conflict may activate ACC in the same way that response conflict on a go/no-go task does, but may have a more emotional component as the different options are weighed against the costs, rather than comparing two motivationally irrelevant response choices. Nevertheless, it will also be important to figure out what the source of resource depletion is, and if it is truly a metabolic phenomenon (Gailliot et al., 2007). In this respect, it is interesting that the anterior cingulate has been implicated in metabolic regulation (Teves et al., 2004).

For larger goals to have influence on behavior, it is often beneficial to break them down into manageable smaller goals. Frontopolar cortex has been implicated in subgoal processing (Braver & Bongiolatti, 2002). This is similar to Gollwitzer's (1999) conception of goal intentions and implementation intentions. It is all very well to have a larger goal in mind, but without breaking it down into the necessary elements that direct behavior in specific ways, it is harder to execute. Implementation intentions are like subgoals, in that they specify how the larger goal should be pursued, but they are also special for another reason. The specific intention is paired with an external cue, such that it is executed when the external cue is encountered in the environment. This takes the pressure off the individual to internally cue the behavior. This is similar to research on prospective memory, while not reviewed here, involves the active maintenance of an intention (pick up dry cleaning) that is made easier if it is paired with a highly salient cue (when you see the red barn from the highway, take the exit for the dry cleaners) (Einstein & McDaniel, 2005). Thus, it may be that frontopolar cortex is engaged under conditions for which implementation intentions are not externally available, and must instead be endogenously generated based on goal intentions.

Another cognitive theory related to reliance on external cues is the dual mechanisms of control theory (Braver et al., 2007, 2009). Proactive control involves utilizing actively maintained context information to prime response selection. Thus, a proactive control strategy would keep the intention of going to the dry cleaners active all day until you arrived there. In contrast, reactive control involves utilizing context information only when needed. Thus, until the red barn was spotted from the highway, the intention would not be activated. Proactive control is generally very successful, but reactive control is less costly because the information only needs to be retrieved when triggered by an imperative event. Thus, the effect of a shift in motivational priority might have the effect of shifting individuals from a reactive cognitive control strategy into a more proactive one.

Other social psychology perspectives emphasize not just how goals are pursued, but how the types of goals people tend to adopt influence their behavior. One theory of goal choice is the research on performance versus mastery goals (Dweck, 1986). Results from many studies show that mastery goals tend to be associated with more positive outcomes. Mastery goals emphasize learning to do a task well rather than comparing your performance to others, and may be more effective exactly because they involve focusing attention on aspects of the task that can be improved. An individual's own behavior is under his or her control whereas others' is not. In addition, "Do better than person X" is more of a goal intention, whereas learning to do the task may be more of an implementation strategy. Thus, other-focused goals may be more cognitively effortful, and require the involvement of higher-order control mechanisms such as the frontopolar cortex.

Although goal choice is important, in laboratory settings the goal is often provided by the experimenter explicitly. When researchers provide incentives, the expectation is that these rewards or punishments (what's at stake) would be actively maintained by participants as they do the task. Evidence reviewed above showed that OFC, and LPFC maintain this kind of information about motivational context with reference to the desires of the individual. This kind of information could be the raw material for goals, as once the individual decides that a reward is worth pursuing (the receipt of the reward is of higher value than the effort required to achieve it), its attainment becomes a goal that is maintained. Given that at the outset of experiments, participants do not have direct experience of how much joy they will get out of a reward, these representations are predictions to some extent. Moreover, even after repeated experience with rewards, the hedonic qualities of these rewards may change (or be state-dependent), and thus it is important to have a maintained representation that captures the most recent experience rather than a more generic long-term memory trace or future prediction. The research on affective forecasting intersects here because it states that individuals decide on what goals to adopt based on their expected amount of positive affect from achieving them. Interestingly, this research has also shown that people are not particularly good at predicting how happy, or upset, they will be in future when they receive a reward or punishment. Thus, the biased predictions of participants may tend to enhance the effects of incentives, as individuals usually exaggerate how happy they will be on receiving a reward, and exaggerate how unhappy they will feel when penalized.

The way that people adopt, pursue, monitor, and react to achieving or failing to achieve goals may strongly relate to individual differences. People differ in how reactive they are to rewards and punishments, and what kinds of goals they feel are important to pursue. These differences may relate to physical differences in the brains of individuals. One theory that connects individual differences in personality to the physical structure of the brain has been conceptualized by Depue and Collins (1999). Their theory equates the functionality of the dopamine circuitry in VTA and NAcc with behavioral approach, such that high levels of DA facilitate approach behaviors aimed at bringing the organism in contact with reward stimuli. In this theory, genetic differences in the number of dopaminergic synapses at birth predisposes individuals with higher numbers of these synapses to explore more for rewards. Contact with more rewards then makes frequent use of the dopaminergic reward system, which leads to less pruning of these synapses, and thus to stable individual differences in the function of the dopamine system. People with greater amounts of dopaminergic activity may then be more reactive to cues of potential rewards, akin to the personality difference reflected in Jeffrey Gray's BAS. Linking this idea to Berridge's work, Depue & Collins state that greater dopaminergic activity may lead to greater incentive salience being attached to objects in the environment. That information could be stored in memory, and retrieved by the prefrontal cortex to motivate behavior even in absence of cues in the environment.

Although it has been less studied, it may be that processing of aversive stimuli and penalties may be subject to individual differences in the structure of the serotonergic system. Recent work in behavioral genetics has looked at variants of a gene that affects a serotonin transporter, 5-HTT. This transporter is situated on the presynaptic neuron, and is responsible for the reuptake of serotonin from the synapse (Hariri & Holmes, 2006). Individuals who have one or two copies of the "short" form of the allele reuptake serotonin less efficiently. Recent studies have examined the effect of this genetic variation on behavior. Individuals with short form 5-HTT are more likely to have higher levels of trait anxiety and harm avoidance (Lesch et al., 1996), have less capacity to cope with stress (Caspi et al., 2003), and show greater amygdala activity in response to fearful and angry faces (Hariri et al., 2002). Together, these results suggest that individuals who have the short allele version of the 5-HTT polymorphism may be more sensitive to cues indicating the possibility of punishments or other aversive outcomes.

In summary, the process by which people set and pursue goals can be studied both by asking about what those goals are, how people feel about them, and what behaviors they exhibit from a macro-level in the social-personality realm, or at the micro-level in cognitive and affective neuroscience research. Some of the concepts generated are similar, and may rely on the same underlying brain structures. More power to interpret the brain activity arising from those structures may be forthcoming if efforts are made to understand motivation on multiple levels.

FUTURE DIRECTIONS FOR RESEARCH

There are several key questions deserving of future research efforts that might be considerably more tractable using a multilevel approach. The first question is how motivation is created in individuals, in order to inspire greater effort to achieve a particular goal. One contributing set of factors is the incentive structures that are used. Research on animals often uses primary rewards, food or drink, whereas research on humans has used a number of different secondary or abstract rewards such as cash, or points. As described above, there is relatively less research on punishments, and less still that directly compares matched rewards and punishments.

Another set of factors is individual differences in participants in reward and punishment sensitivity, some of which are traceable to differences in brain anatomy and physiology. A combination of self-report or physiological measures on incentive-related variables and neuroimaging that can noninvasively reveal differences in the structure and function of relevant brain regions has the potential to quantify differences among participants.

To answer questions about how incentives and individual differences affect the creation of motivation, a good first step would be to have a picture of what reward and punishment motivational states look like in terms of their effects on behavior and brain activity. Understanding simple motivational states will then allow research to advance to look at how variations in incentives or the type of participants tested affects motivation. This research requires expertise in both psychometrics and neuroimaging, and is a prime candidate for interdisciplinary cooperation.

A second question for future research concerns how motivation, once created, affects cognition and action. How does having greater motivation facilitate the pursuit of goals? Looking at how the brain responds to incentives has yielded an important distinction between valence-dependent activity, which reflects the value of the incentives, and activity generated equally by both negative and positive incentives (valence-independent activity) (Roesch & Olson, 2004). On the valence-dependent side, research on reward processing has shown the complexity of reward representations. Specifically, rewards are evaluated for their magnitude, and their value to the individual in general (trait preferences, e.g., for certain foods) and at the time they are offered (state preferences, e.g., whether the person is hungry or not).

On the valence-independent side, there are prefrontal cortex neurons that respond just as strongly to high positive as high negative incentives, suggesting a translation has taken place that has stamped particular actions as important. Once a particular task has been deemed important, the next step is to translate desire to achieve a goal into action items. This process may be critical, and may be where some people who seem very motivated and/or report a high value on incentives fail. Recognizing importance per se is not sufficient, as shown by Gollwitzer's work contrasting goal intentions, which are vague goals like "do better in school," and implementation intentions, that explicate the goal with specific steps which are linked to external cues ("When I get home from school each day, I will spend an hour reading.").

A final question relates to how these two systems--that extract the value of different incentives, and then translate this information into specific action goals—interact to facilitate goal selection, and set effort levels for goal pursuit. To study this question, one strategy would be to design experiments where participants are presented with tasks that vary according to both the potential incentives possible (e.g., manipulate incentive valence and incentive value), and the actions or task dimensions to which they are attached. Ideally, these manipulations would be factorial (i.e., independent of each other). Given a task with a well-known behavioral and brain activity profile, it would be possible to see how the presence of incentives affects how people engage in the task, and whether these modulatory influences interact with either (or both) incentive manipulations or task goal manipulations.

The major questions outlined in this section about the creation of motivation, and the downstream effects of motivation, necessarily interact. For example, given that there are important individual differences in how participants react to the presence of reward and penalty cues, information from the valence-dependent system will be different for a participant who is indifferent to incentives than it will be for a participant strongly affected by incentives. In terms of channeling motivational drive into appropriate action, there may also be important differences in the capacity to break larger goals down into smaller, intermediate steps, perhaps related to working memory capacity or fluid intelligence.

Conclusion

Studying motivation, from its creation to how it affects brain activity and cognition, to ultimate changes in behavior, is an endeavor that requires consideration of multiple levels of analysis. In particular, motivation can be thought of as reflecting a process that sets the priority value of different behavioral goals, and hence the effort that will be expended to achieve them. This process affects goals and behaviors that span the range from primary drives and behaviors, such as eating and drinking, to future plans that may take years to complete (i.e., obtaining a Ph. D.). Thus, the factors that affect these goal priority mechanisms must involve computations that span the range from low-level assessments of physiological state (e.g., hunger), to complex and abstract evaluations of the cognitive demands and contextual constraints (e.g., social) of the current situation, as well as any stable trait-like differences in reactivity to these different variables. Consequently, a better understanding of the mechanisms of motivation and their influence on information processing may provide a crucial leverage point for researchers interested in self-control from various perspectives and domains of inquiry.

This chapter has reviewed work on, and theories of, motivation arising from both the neuroscience and social/personality literatures. We have further argued that a cognitive neuroscience approach may be particularly suited to helping close the gap between these two perspectives by providing hypotheses about the contributions of specific brain regions to cognitive processes that underlie the performance of tasks under incentive conditions, and how these are affected by both situational (i.e., task-related) and personality variables. It is our belief that future developments in the cognitive neuroscience of motivation will contribute strongly to a better understanding of the nature of self-control, by shedding light on the core processes that modulate the selection and pursuit of behavioral goals—the achievement of which is the hallmark of successful self-regulation.

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