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Reward Processing

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Synopsis

Our behavior is inextricably linked to rewards in our environment. This observation has sparked considerable interest in understanding the neural mechanisms that support reward processing in humans. Early neuroimaging studies implicated regions such as the striatum and ventromedial prefrontal cortex (VMPFC) in reward processing, particularly how activation in these regions is modulated by anticipation and receipt of rewards. These findings have been extended in the context of models that account for the representation of subjective value, which influences decision making. Building from these findings, researchers are now beginning to characterize how social information has idiosyncratic influences on reward processing.

Introduction

Our decisions frequently require us to evaluate and compare available rewards in the environment. Broadly defined, rewards are stimuli of positive valence that have the potential to influence behavior (for additional information, see §58 Reward). Refining this definition, animal learning theory notes that rewards function to promote learning, encourage approach and consummatory behavior for acquiring reward items, and induce positive emotions (Berridge & Robinson, 1998; Robbins & Everitt, 1996; Schultz, 2006). Notably, deficits in these functions are hallmarks in several psychopathologies ranging from schizophrenia (Gold et al., 2012) to depression (Pizzagalli et al., 2009) (for additional information, see §116 Schizophrenia, and §119 Depression). Thus, understanding the neural mechanisms supporting reward processing has been a long-standing objective in neuroscience. Although considerable progress toward this objective has been made using a wide range of methodologies and approaches—including single-unit neurophysiology (Hayden et al., 2009; Sugrue et al., 2005), optogenetics (Stuber et al., 2012), and brain stimulation (Amemori & Graybiel, 2012; Boggio et al., 2010)—this chapter will primarily focus on findings from human neuroimaging work.

To investigate reward processing, researchers have employed concrete rewards such as money (Delgado et al., 2000; Knutson et al., 2001) and food (Kringelbach et al., 2003; Small et al., 2001), as well as more abstract rewards such as social status (Ly et al., 2011) and attractive faces (O'Doherty et al., 2003a; Winston et al., 2007). Yet, we note that some reward processing studies have utilized aversive outcomes (e.g., an electric shock) that subjects aim to avoid (Delgado et al., 2009; Kim et al., 2006). Though interesting in its own right, the rewarding properties of avoiding aversive outcomes is beyond the scope of this chapter, so we refer readers to relevant reviews (Bromberg-Martin et al., 2010; Delgado et al., 2008a; Seymour et al., 2007b). The bulk of studies reviewed in this chapter will be limited to stimuli with a clear positive valence that can be easily studied in within the constraints of the neuroimaging environment using human subjects.

Studies of reward processing have implicated a diverse set of brain regions, particularly the ventromedial prefrontal cortex (VMPFC) and striatum. Indeed, a large-scale automated meta-analysis (Yarkoni et al., 2011) of 203 neuroimaging studies demonstrates a selective association between the term “reward” and activation in VMPFC and striatum (Figure 1). Although these regions are likely fundamental to reward processing, we note

that other studies have found links between activation in amygdala ([Jenison et al., 2011](#); [Morrison & Salzman, 2010](#)), midbrain ([Ballard et al., 2011](#); [Carter et al., 2009](#); [D'Ardenne et al., 2008](#)), and parietal cortex ([Klein et al., 2008](#); [Platt & Glimcher, 1999](#)). The putative reward circuit in humans therefore involves several regions, chief among them are the VMPFC and striatum. Accordingly, many of the studies reviewed in this chapter will focus on VMPFC and striatum due to a larger wealth of data on reward processing and these regions.

Foundations of Reward Processing

Early investigations of reward processing were spurred by the observation that rats would work vigorously—often while sacrificing food—to electrically self stimulate near the ventral striatum (Olds & Milner, 1954). Similar observations were made in human subjects, who reported sensations of pleasure upon receiving electrical stimulation to an area near the ventral striatum (Bishop et al., 1963). These studies suggested that dopamine, a neuromodulator originating in the midbrain and projecting to the striatum ([Haber & Knutson, 2010](#)), might be inextricably linked to reward processing. This idea inspired pharmacological work that directly manipulated the levels of dopamine in rodents. Strikingly, researchers observed that animals deficient in dopamine showed attenuated reward-related responses, such as reduced response rates and diminished interest in food and sex ([Wise et al., 1978](#)). Although these observations led to popular accounts of dopamine functioning as a “pleasure chemical”, some work has questioned whether dopamine is even necessary for reward processing or the experience of pleasure (Cannon & Bseikri, 2004). Furthermore, subsequent studies have indicated that dopamine serves wider functions related to motivated behavior, including altering the salience of incentives ([Berridge & Robinson, 1998](#)) and updating models of reward prediction ([Schultz & Dickinson, 2000](#)).

Adapting behavior based on models of predicted rewards serves as an important function of reward processing, as it affords an opportunity to maximize future rewards. Reward prediction errors (RPEs) occur when a stimulus alters our expectations of the content of future rewards ([Schultz, 2000](#); [Schultz & Dickinson, 2000](#)) (for additional information, see §257 Reinforcement Learning). To investigate the neuronal basis of RPE signals, Schultz and colleagues ([Schultz et al., 1997](#)) utilized single-unit recordings and measured how midbrain activity changed in response to a cue that predicted a reward. At the beginning of the experiment, prior to learning the cue-reward association, midbrain neurons exhibited increased firing rates in response to the unexpected reward but not the cue. Over time, as the cue-reward association became stronger, cue-evoked activity increased while reward-evoked activity diminished. Once the cue-reward association became fully established, the omission of a predicted reward led to diminished midbrain activity. Based on these findings, Schultz and colleagues put forth the hypothesis that dopaminergic neurons within midbrain encoded RPE signals ([Schultz, et al., 1997](#)). Similar RPE signals have been observed to correlate with activity in areas that receive dopaminergic projections from the midbrain, such as the VMPFC ([Ramnani et al., 2004](#); [Rutledge et al., 2010](#)) and striatum ([O'Doherty et al., 2003b](#); [Rutledge, et al., 2010](#)).

Although the relationship between RPE signals and key dopaminergic areas such as VMPFC and striatum is now well established, other work has suggested additional reward processing functions for these regions, particularly the anticipation of and receipt of rewards. To examine how the brain encodes the anticipation of and receipt of rewards, Knutson and colleagues ([Knutson, et al., 2001](#)) developed a response-time task (the Monetary Incentive Delay or MID task). On a typical trial of the MID, subjects first see a cue indicating the type and magnitude of a reward (e.g., \$5). Then, after a brief and variable anticipatory period, a target appears. If the subject responds to the target quickly enough, the reward is delivered. This approach yielded two core results: reward anticipation increased in ventral striatum while reward receipt increased activation in VMPFC ([Knutson et al., 2003](#)).

Other studies of reward processing have utilized alternative task structures, including active decision making such as gambling games ([Breiter et al., 2001](#); [Delgado, et al., 2000](#); [Elliott et al., 2000](#)). For example, Delgado and colleagues ([Delgado, et al., 2000](#)) created a simple card-guessing task in which each trial asks the subject to guess whether an upcoming card will be higher or lower than the number 5. Correct guesses earn a monetary reward whereas incorrect guesses result in a monetary punishment. Using this simple structure, Delgado and colleagues found that monetary rewards compared to punishments evoke activation in the striatum ([Delgado, et al., 2000](#)). As these observations could reflect the affective qualities of reward, [Tricomi and colleagues \(Tricomi et al., 2004\)](#) investigated whether the reward-related signal observed in the dorsal striatum is due to the hedonic aspect of a reward outcome or the reinforcement of the action that led to the reward outcome. Crucially, their results indicated that reward-related outcome responses in the dorsal striatum, in particular, are dependent on action, indicating a link between striatal activation and reinforcement. Extending these observations, other researchers have applied reinforcement learning models to striatal activation, noting distinct roles for ventral and dorsal striatum, with the former participating in the prediction of future rewards and the latter maintain representations action-outcome contingencies ([O'Doherty et al., 2004](#)). Yet, even in the absence of learning, other work has highlighted an important role for motivation in striatal activation ([Clithero et al., 2011](#); [Delgado et al., 2004](#)). Taken together, these findings highlight the complexity of striatal reward-related responses, as they represent multiple signals related to value, motivation, and learning (e.g., RPE).

Although much of the work on reward processing in humans has utilized monetary incentives, a host of research point to the general nature of the reward processing system. Activation in striatum and VMPFC is modulated by various sensations, including the taste of chocolate ([Small, et al., 2001](#)) and juice ([Kim et al., 2011](#)), pleasant smells ([Gottfried et al., 2002](#)), touch ([Rolls et al., 2003](#)), and viewing attractive faces ([Aharon et al., 2001](#); [O'Doherty, et al., 2003a](#)), and even the texture of fat in the mouth ([Grabenhorst et al., 2010](#)). These findings also generalize to abstract rewards such as humor ([Mobbs et al., 2003](#); [Watson et al., 2007](#)), art ([Vartanian & Goel, 2004](#)), charitable giving ([Moll et al., 2006](#)), the experience of romantic love ([Acevedo et al., 2012](#); [Aron et al., 2005](#)) and other social stimuli ([Fehr & Camerer, 2007](#)). These observations highlight the general nature and flexibility of the reward circuit, potentially hinting at its significance in shaping behavior in response to diverse stimuli and events.

Encoding the Subjective Value of Rewards

The observation that multiple rewards evoke similar activation within the striatum and VMPFC may hint at a mechanism for flexibly comparing disparate rewards on a common scale ([Grabenhorst & Rolls, 2011](#); [Montague & Berns, 2002](#)). Understanding the neural mechanisms underlying this computation has been a cardinal goal of decision neuroscience ([Padoa-Schioppa, 2011](#); [Rangel et al., 2008](#); [Smith & Huettel, 2010](#)) (for additional information, see §258 Value Representation and §262 Economic Decision Making). To address this goal, several studies have now converged on the observation that VMPFC ([Chib et al., 2009](#); [FitzGerald et al., 2009](#); [Kim, et al., 2011](#); [Lin et al., 2012](#)) and striatum ([Clithero, et al., 2011](#); [Izuma et al., 2008](#)) contain spatially overlapping reward-related signals for multiple reward types (e.g., money, food, social images, and consumer goods). These findings have also been confirmed by meta-analytic techniques aggregating data across multiple studies ([Clithero & Rangel, 2014](#)).

Though suggestive of a mechanism for representing different goods on a common scale, these studies do not consider how individual differences preferences between rewards relates to activation differences for those rewards. If a brain region—whether VMPFC or striatum—encodes a reward signal on a common scale, researchers have hypothesized that activation within that region (or regions) should predict an individual's subjective value for those rewards ([Levy & Glimcher, 2012](#)). Using this general approach, recent research has suggested that activation within VMPFC encodes different rewards on a common scale in which idiosyncratic subjective values (e.g., how much money an individual is willing to spend for a reward) are matched to neural value signals (e.g., the difference in activation magnitude for the good and money) within VMPFC ([Levy & Glimcher, 2011](#); [Smith et al., 2010](#); [Zaki et al., 2014](#)). Extending these observations, recent work has also noted that state-dependent changes in subjective value predict state-dependent changes in VMPFC activation ([Libedinsky et al., 2011](#)). Collectively, these studies suggest that portions of VMPFC compute reward-related signals on a common scale that predicts the subjective value of rewards ([Levy & Glimcher, 2012](#)).

Modulation of Reward Processing by Social Information

Reward-related signals computed in VMPFC and striatum are subject to modulation by multiple factors, including bodily states of satiety ([Gottfried et al., 2003](#)), time ([Kable & Glimcher, 2007](#)), and social information ([Behrens et al., 2008](#)). The effect of social information on reward processing is greatly facilitated by human neuroimaging studies, as they allow for real-time interaction between subjects. Using this approach, King-Casas and colleagues observed that signals to trust a partner are encoded like RPEs such that, over time, learning that a partner predicts reward shifts dorsal striatum from the receipt of a monetary reward to the social interaction with the partner ([King-Casas et al., 2005](#)). Multiple studies have now demonstrated that reward-related signals in striatum can be modulated social factors related to competition ([Delgado et al., 2008b](#); [van den Bos et al., 2013](#)) and sharing with a close friend ([Fareri et al., 2012](#)). These findings further highlight the complexity of reward-related signals within striatum, adding to evidence that striatal signals are not solely due to learning, as they can be modulated by factors unrelated to learning and reinforcement (e.g., level of closeness between participants).

To understand the neural mechanisms underlying this modulatory influence, researchers have employed functional connectivity techniques, which quantify how the temporal correlation between distal brain regions changes depending on the psychological task (e.g., gaining or losing money) ([Friston et al., 1997](#)) (for additional information, see §212 Functional Connectivity). One key hypothesis asserts that regions modulated by social cognitive processes ([Behrens et al., 2009](#); [Saxe, 2006](#)) (for additional information, see §172 Social Cognition During Social Interactions), particularly the temporal-parietal junction ([Carter et al., 2012](#)), should exhibit increased functional connectivity with regions modulated by reward processing. Supporting this prediction, recent research has shown that functional connectivity between VMPFC and regions within the inferior parietal lobe, including the TPJ, increases during empathy ([Janowski et al., 2013](#)), charitable donations ([Hare et al., 2010](#)), attractive judgments ([Smith et al., 2014](#)), and social competition ([van den Bos, et al., 2013](#)). However, it should be noted that functional connectivity techniques cannot test for directionality. Thus, in these studies, it remains unclear whether signals in TPJ are directly influencing reward-related signals in VMPFC. Nevertheless, these observations provide a promising avenue for understanding how reward processing can be modulated by social information.

Conclusions and Future Challenges

The study of human reward processing has consistently demonstrated that the striatum and VMPFC are core components of our reward circuitry. Our understanding of this circuitry has rapidly evolved over the past decade. Early demonstrations of how the anticipation of and receipt of rewards modulates activation in the VMPFC and striatum have now developed into complex models of subjective value that shape idiosyncratic choice behavior. Researchers are also beginning to understand how social information impacts reward processing, potentially through functional interactions with regions outside typical reward circuitry.

Despite this progress, several challenges remain. For example, some researchers argue that reward and attention are frequently confounded, thus creating interpretative challenges for reward-related signals ([Maunsell, 2004](#)). In addition, previous reports have led to conflicting results on whether striatum encodes salience ([Jensen et al., 2007](#); [Zink et al., 2006](#)), valence ([Delgado, et al., 2000](#); [Seymour et al., 2007a](#)), or both ([Cooper & Knutson, 2008](#); [Litt et al., 2011](#)). Recent work has also suggested that reward-related signals are distributed throughout the gray matter ([Vickery et al., 2011](#)). These issues underscore the importance of examining different components of reward that are typically conflated in most paradigms. For example, most rewarding events carry affective properties that signal valence (e.g., whether the outcome was good or bad) and informative properties that signal how to maximize future rewards (e.g., repeat this action to get another reward). Indeed, recent research has highlighted how information in itself evokes activation in the reward circuitry ([Bromberg-Martin & Hikosaka, 2011](#); [Tricomi & Fiez, 2012](#)). Parsing reward into different subcomponents (e.g., affective and informative) may facilitate translational work that seeks to ameliorate dysfunctional reward processing in psychopathologies ([Treadway & Zald, 2013](#)). Taken together, these challenges—and their

potential remedies—pave the way for years of fruitful studies on the mechanisms of reward processing.

Figure Caption

Figure 1: Brain Regions Involved in Reward Processing

A large-scale meta-analysis of 203 studies using the term “reward” reveal a strong association between activation in the ventromedial prefrontal cortex (VMPFC) and striatum. Activation in these regions is thus highly predictive of reward. Image is thresholded at whole-brain corrected (false discovery rate) at $p < 0.05$.

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