EMOTION, DECISION-MAKING AND THE BRAIN

Luke J. Chang and Alan G. Sanfey

ABSTRACT

Purpose – Initial explorations in the burgeoning field of neuroeconomics have highlighted evidence supporting a potential dissociation between a fast automatic system and a slow deliberative controlled system. Growing research in the role of emotion in decision-making has attempted to draw parallels to the automatic system. This chapter will discuss a theoretical framework for understanding the role of emotion in decision-making and evidence supporting the underlying neural substrates.

Design/Methodology Approach – This chapter applies a conceptual framework to understanding the role of emotion in decision-making, and emphasizes a distinction between expected and immediate emotions. Expected emotions refer to anticipated emotional states associated with a given decision that are never actually experienced. Immediate emotions, however, are experienced at the time of decision, and either can occur in response to a particular decision or merely as a result of a transitory fluctuation. This chapter will review research from the neuroeconomics literature that supports a neural dissociation between these two classes of emotion and also discuss a few interpretive caveats.

Findings – Several lines of research including regret, uncertainty, social decision-making, and moral decision-making have yielded evidence

consistent with our formulization—expected and immediate emotions may invoke dissociable neural systems.

Originality value—This chapter provides a more specific conceptualization of the mediating role of emotions in the decision-making process, which has important implications for understanding the interacting neural systems underlying the interface between emotion and cognition—a topic of immediate value to anyone investigating topics within the context of social-cognitive-affective-neuroscience.

INTRODUCTION

The nascent field of neuroeconomics promises to deliver novel insights into everyday choice behavior by integrating the theories and methodologies from the diverse fields of psychology, economics, and neuroscience (Glimcher & Rustichini, 2004; Montague, King-Casas, & Cohen, 2006; Sanfey, Loewenstein, McClure, & Cohen, 2006). This approach attempts to merge economic principles, built on formal mathematical models, with measures of brain function using in vivo techniques such as single and multi-unit neuronal recordings, functional magnetic resonance imaging (fMRI), and more traditional neuropsychological methods that rely on patients with focal brain lesions. While the details of how these methods can be successfully integrated are still being developed, there have already been several interesting avenues of research (McCabe, Houser, Ryan, Smith, & Trouard, 2001; McClure, Laibson, Loewenstein, & Cohen, 2004; O'Doherty et al., 2004; O'Doherty, Hampton, & Kim, 2007; Sugrue, Corrado, & Newsome, 2005; Yechiam, Busemeyer, Stout, & Bechara, 2005), suggesting that the neuroeconomic endeavor can have a real impact in better understanding how we make choices and decisions.

One of the most promising of these directions is the notion that the brain may utilize specific subsystems when making judgments and decisions (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001; McClure et al., 2004; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). The idea of the involvement of multiple systems in the processing of complex cognitions has a long history, dating back to the fathers of modern day psychology, including Descartes (Descartes, 1664), Wundt (Blumenthal, 1980), and James (James, 1890). This insight of William James, that decisions could be made via both automatic and controlled processes, has continued to intrigue researchers to this day. In fact, many proposed theoretical models utilize

this notion of multiple systems (Chaiken & Trope, 1999; Epstein, 1994; Evans & Over, 1996; Hammond, 2000; Kahneman, 2003; Sanfey & Chang, 2008; Schneider & Shiffrin, 1977; Sloman, 1996; Stanovich & West, 2000).

Though each of these theories differs in implementational details, they all generally propose a dual-process model of decision-making, with two distinct systems that alternatively compete and cooperate to arrive at a decision (Poldrack & Packard, 2003). System 1 has consistently been described as automatic, fast, effortless, unconscious, associative, slow-learning, and emotional. System 2 can best be thought of as more controlled, slow, effortful, conscious, rule-based, fast-learning, and affectively neutral. System 1 processes are generally thought to underlie most of our more trivial decisions, where automatic responses are adaptive. System 2, which is typically more computationally demanding (Schneider & Chein, 2003), is available to monitor and potentially override System 1 when the automatic system requires more conscious control (for a more detailed review see (Sanfey & Chang, 2008). For example, when learning to drive an automobile, one's actions are largely in the control of System 2, with conscious controlled attention directed to the act of learning to operate a vehicle. With practice, many of these motor tasks become increasingly automatized under the control of System 1, which allows us to direct our attention towards conversation with passengers, listening to the radio, etc.

Standard models of decision-making have typically focused on System 2-type operations, namely the deliberative process of careful decision-making. In recent years, however, there has been a considerable effort to better specify the extent to which affective processes, such as those encompassed in System 1, can influence judgments and decisions. Traditionally, emotions have been outside the purview of decision-making researchers, and indeed emotions have often been proposed to be counterproductive to sensible decision-making. For example, we are often exhorted not to make decisions in the heat of the moment, and to cool down before making important choices. However, it is often the case that emotions may provide important signals to lead us to making more optimal decisions in certain circumstances.

Use of emotions in decision-making can have functional significance in learning what can be approached and what should be avoided (Davidson, 1995). Early work in this domain by neurologists revealed that patients who had suffered brain damage leading to impaired emotional processing often made suboptimal decisions as compared to emotionally intact controls (Bechara, Damasio, Tranel, & Damasio, 1997; Damasio, 1994). This was the

first real empirical evidence suggesting that emotional processes may play a benevolent role in guiding decisions, and has since led to a growing literature on this topic. Other recent work has proposed the existence of the affect heuristic (Loewenstein, Weber, Hsee, & Welch, 2001; Slovic, Finucane, Peters, & MacGregor, 2002), by which we use the natural assessments of affective valence as the basis for judgments. These studies have largely discounted the notion that System 1 is naturally "irrational," and that System 2 provides the only set of processes capable of sensible decisions. Clearly, there is a complex exchange between these systems, and much further research will be needed before clearly defined boundaries between these systems are revealed, if indeed such boundaries exist. It is important to note at the outset that it is still largely unknown to what degree these systems are separable at the neural level. It seems very unlikely that these are two biologically distinct processes (Glimcher, Dorris, & Bayer, 2005), but evidence has shown that some degree of functional specialization may exist in the brain to distinguish the two types of processes.

The early research mentioned above used patients who had suffered brain injuries to examine the influence of emotions in decision-making. This approach is problematic for various reasons, including the heterogeneity of lesion locations, the possibility of brain damage to other areas, etc. The recent availability of brain imaging techniques that allow visualization of the normal, active human brain has allowed a wide variety of questions to be explored as to the involvement of emotions in decision-making.

The present chapter will discuss the neural underpinnings of emotion's influence on decision-making. The chapter will begin with a brief overview of how emotions are processed in the brain, highlighting key regions of interest. Next, a framework for conceptualizing emotions in the context of decision-making will be introduced. This conceptual framework, originally proposed by Loewenstein and Lerner (2003), makes an important distinction between expected and immediate emotions. The neural evidence supporting such a distinction will be evaluated using recent findings from neuroeconomic studies investigating regret, uncertainty, social decision-making, and moral decision-making. Finally, we will conclude with an integrative summary of all of the findings, noting a few interpretive caveats.

HOW THE BRAIN PROCESSES EMOTION

The study of emotion has traditionally focused on cognitive appraisals and physiological mechanisms. In recent years, however, there has been significant interest in assessing the neural response to emotional processing. One of the oldest debates in the emotion literature is whether or not the physiological responses associated with an emotional reaction precede the cognitive appraisal. William James (1884) and Carl Lange (1887) independently proposed that in response to a fearful stimulus, such as meeting a bear in the woods, the cognitive appraisal of fear will occur *after* the body has already physiologically responded to the situation. This response might take the form of a racing heart, hyperventilation, or fleeing the scene. Other theorists proposed that it was not possible to have a physiological response without the cognitive appraisal (Lazarus, 1982; Schachter & Singer, 1962). More recently, researchers have come to accept that both theories seem to be correct. The differentiation between these two responses is often referred to as either bottom-up or top-down processing. A bottom-up response is when the physiological response precedes the cognition, and a top-down response is when the cognitive appraisal leads to a physiological response.

Both of the aforementioned processes seem to have pathways in the central nervous system. For example, specific facial motor functions, like smiling, may have multiple innervations (Duchenne, 1862). Numerous cases have demonstrated that selective damage to either pathway spares the function associated with the other (Holstege, 2002; Trosch, Sze, Brass, & Waxman, 1990). Other physiological functions associated with emotion, such as respiration and heart rate, also seem to be regulated both involuntarily, via programs located in the brainstem, and voluntarily, through cortical input originating from the anterior cingulate cortex (ACC; Critchley et al., 2003; McKay, Evans, Frackowiak, & Corfield, 2003). The following section will present a brief overview of brain regions associated with emotional processing (see Fig. 1). For the purposes of this review, we will focus on negative emotions, such as fear and disgust. Investigations of this class of emotions have been considerably more extensive than studies of positive emotions. The primary reasons are that negative emotions are more straightforward to investigate in animals and can be extracted with relative ease in laboratory studies.

One emotion that has received extensive empirical investigation is fear. The experience of fear usually begins with a freezing response, a subsequent sympathetic response, and an increase in sensory perception. This allows the environment to be adequately surveyed before a fight or flight response is taken. Fear has been proposed to employ two distinct streams of processing operating in parallel. These two streams allow both a physiological response and a simultaneous cognitive appraisal (Ledoux, 1996). In the controlled
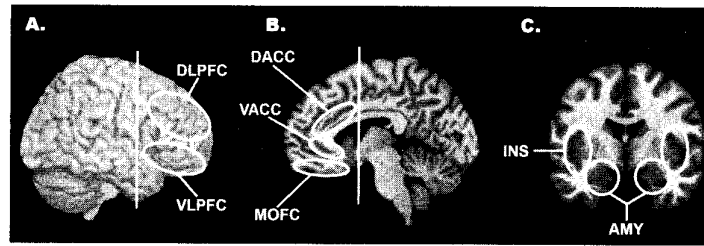
Fig. 1. Brain Areas Involved in Emotion Processing and Decision-Making. (A) The Lateral View Shows the Locations of the Dorsolateral Prefrontal Cortex (DLPFC) and Ventrolateral Prefrontal Cortex (VLPFC). Also Referred to as Lateral Orbitofrontal Cortex (LOFC). (B) The Saggital Section Shows the Locations of the Dorsal Anterior Cingulate Cortex (DACC), Ventral Anterior Cingulate Cortex (VACC), and Medial Orbitofrontal Cortex (MOFC). (C) The Coronal Section Shows the Locations of Bilateral Insular Cortex (INS) and the Bilateral Amygdalae (AMY). The Location of the Coronal Section is Indicated on the Lateral and Saggital Views by the White Vertical Line.

cortical route, information travels from the retina to the lateral geniculate nucleus of the thalamus and terminates in the contralateral primary visual cortex (Zeki, 1993). Visual information is then transmitted to the surrounding extrastriate cortex for further processing. The more controversial automatic subcortical pathway has been described as the "quick and dirty" route. It bypasses the visual cortex by traveling directly from the retina to the superior colliculus, then to the pulvinar (the posterior part of the thalamus) and amygdala, and then projecting to visual association cortex (Ledoux, 1996).

Overwhelming evidence suggests that the amygdala, a small almond shaped structure located in the medial temporal lobe (Aggleton, 1992), is essential to fear processing (Adolphs, Tranel, Damasio, & Damasio, 1994; Isenberg et al., 1999; LaBar & Cabeza, 2006; Ledoux, 1996; Morris et al., 1998; Phelps & LeDoux, 2005; Phillips, Drevets, Rauch, & Lane, 2003; Whalen et al., 1998). This makes sense from a neural framework as it is situated in a place such that it can receive higher-order inputs from multiple streams of cortical processing and signal autonomic responses in the hypothalamus to prepare the body for fight or flight.

Another negative emotion that has been reliably associated with a specific neural substrate is disgust (Calder, Lawrence, & Young, 2001; Phillips et al., 1997). Disgust is typically associated with stimuli that are revolting,

inedible, or impure, and has been found to be associated with a region of the brain called the insula. The insula processes taste and smell information (Nolte, 2002; Small et al., 1999), as well as somato-visceral states of the body, such as pain, temperature, and "gut-feelings" (Craig, 2002). The insula has also been found to be associated with the experience of moral disgust (Haidt, 2001; Moll et al., 2005), autonomic arousal (Critchley, Elliott, Mathias, & Dolan, 2000), and in self-generated experiences of anger (Damasio, Grabowski, Bechara, & Damasio, 2000). Lesions to the insula can disrupt taste aversion in rats (Dunn & Everitt, 1988) and impair the recognition and experience of disgust (Calder, Keane, Manes, Antoun, & Young, 2000; Phillips et al., 1997) and other somato-sensory cravings in humans (Naqvi, Rudrauf, Damasio, & Bechara, 2007). The famous neurosurgeon Wilder Penfield found that stimulating the insula of patients during surgery led to the experience of nausea and unpleasant tastes (Penfield & Faulk, 1955). Antonio Damasio and his colleagues have proposed that the insula may be associated with the conscious experience of somatic states, and that it represents the influence of "gut-feelings" on decision-making (Bechara et al., 1997; Damasio, 1994; Naqvi et al., 2007).

The amygdala and insula have both direct and indirect reciprocal connections with regions that are associated with more cognitive functions in the prefrontal cortex (PFC). The ability to represent value and evaluate outcomes is thought to be associated with the medial orbital frontal cortex (MOFC; Gottfried, O'Doherty, & Dolan, 2003; Knutson, Adams, Fong, & Hommer, 2001; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001), while the ability to override responses is associated more with lateral orbital frontal cortex (LOFC; Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Garavan, Ross, Murphy, Roche, & Stein, 2002). The more dorsal regions of the lateral prefrontal cortex (DLPFC) are important in maintaining and manipulating information (Baker, Frith, Frackowiak, & Dolan, 1996) and are associated with cognitive appraisals and goal maintenance (Miller & Cohen, 2001). The dorsal anterior cingulate cortex (DACC) is involved with a number of functions, including directing attention, monitoring error, and response override (Carter et al., 1998; Devinsky, Morrell, & Vogt, 1995; Miller & Cohen, 2001; Posner & Dehaene, 1994). The ventral anterior cingulate cortex (VACC) has been hypothesized to be associated with assessing the salience of emotional information and regulating emotional responses (Bush, Luu, & Posner, 2000; Devinsky et al., 1995; Drevets, 1999; Mayberg et al., 2005).

In summary, negative emotions such as fear, disgust, and anger have been reliably associated with distinct substrates of the brain, including the

amygdala, insula, MOFC, and VACC. These regions process somatic states and signal physiological responses associated with arousal via the hypothalamic-pituitary axis. Likewise, they process higher-order cortical processes located in the LOFC, DACC, and DLPFC that can both up-regulate and down-regulate the emotional response. While these functions have traditionally been associated with basic emotion processing, recent evidence suggests that they may also be involved in more complex cognitive processes such as decision-making.

EMOTIONAL PROCESSES IN DECISION-MAKING

The impact of emotions on decision-making has been reviewed extensively elsewhere (Bechara, Damasio, & Damasio, 2000; Loewenstein & Lerner, 2003; Loewenstein et al., 2001; Mellers, Schwartz, & Ritov, 1997; Schwarz, 2000; Slovic et al., 2002); therefore, we will summarize here only the relevant work which has been studied in a neuroeconomic context. One useful framework for organizing the impact of affect on decision-making is to distinguish between expected and immediate emotions (Loewenstein & Lerner, 2003). Expected emotions are those that, while not experienced directly at the time of decision, are nonetheless important in the decision process itself. For example, when assessing a potentially risky investment, we may anticipate the regret we might feel should the investment fail. This anticipation of regret may in turn lead us to take the decision to avoid that financial opportunity. Immediate emotions, however, are those that are directly experienced at the time of the decision. Immediate emotions can have both direct and indirect effects on decision-making. Emotions that have direct effects can be considered "anticipatory" emotions. These emotions are experienced in anticipation of the actual decision and can include feelings of anxiety (Loewenstein et al., 2001; Slovic et al., 2002), dread (Berns et al., 2006), or excitement (Knutson, Fong, Bennett, Adams, & Hommer, 2003). Emotions that have indirect effects are referred to as "incidental" emotions. They include transient mood states that may be unrelated to the decision process, but nevertheless impact choice behavior.

Isen (2000) has shown that positive moods can lead to higher levels of risk aversion, increased reliance on heuristics, and increased efficiency in the decision-making process. Others have reported that experimentally induced incidental emotions, like sadness, can cause subjects to behave in ways that are more economically optimal, such as lessening the well-characterized endowment effect (Lerner, Small, & Loewenstein, 2004). The following sections will review the neural evidence supporting a distinction between expected and immediate emotions in the context of decision-making.

NEURAL EVIDENCE OF EXPECTED EMOTIONS

Expected emotions refer to the predicted emotional consequences associated with the result of a particular decision. These predicted emotional consequences can be positive or negative, and can therefore influence the decision accordingly. Expected emotions can be considered a top-down influence on behavior, as they are a cognitive representation of a future event, which in turn can elicit a physiological response. Previous researchers have hypothesized a dorsal-ventral distinction between the cognitive and emotional regions associated with affect (Bush et al., 2000; Lane, 2000). Candidate regions for expected emotions might include areas associated with goal maintenance and executive control (DLPFC), error or conflict monitoring (DACC), and value representation or outcome evaluation (MOFC). While there are numerous studies that have investigated the neural underpinnings of expected emotion on decision-making, we will focus on the most well studied emotion — regret.

Regret refers to the feeling that one experiences when the outcome of a decision is worse than expected. It differs from disappointment in that it is associated with a sense of personal agency (Bell, 1985; Loomes & Sugden, 1986). It was originally proposed as a way to explain behavioral violations of expected utility theory in decision-making under uncertainty, by incorporating regret minimization into the utility function (Bell, 1982; Loomes & Sugden, 1982). The experience of regret involves making a counterfactual comparison between the outcome actually experienced and an alternative outcome that was rejected (Byrne, 2002), and people generally avoid choice options that are associated with higher anticipated regret (Mellers, Schwatz, & Ritov, 1999; Zeelenberg, Beattie, van der Pligt, & de Vries, 1996). For example, one social psychology experiment found that when students were asked to exchange a lottery ticket they had personally chosen for one with better odds, the majority refused due to the anticipation of regret if their original ticket had won. Other work has demonstrated that regret is distinct from risk aversion (Zeelenberg et al., 1996), and that it can predict post-decisional affect (Mellers et al., 1999).

More recently, regret has been investigated from a neural framework using both lesion methods (Camille et al., 2004) and functional neuroimaging (Coricelli et al., 2005). Both studies utilized a task that has previously

been used to investigate the influence of regret and disappointment on decision-making (Mellers et al., 1999). The task involved making a series of independent choices between two risky gambles that varied in magnitude (e.g. −$200, −$50, +$50, and +$200) and probability (e.g. 20%, 50%, and 80%). The authors elicited regret by disclosing the outcome of the alternative choice. A small actual win (e.g. $50) compared to a large return of the un-chosen option (e.g. $200) was hypothesized to elicit a negative emotional reaction.

Using both subjective ratings and skin conductance, Camille et al. (2004) demonstrated that healthy control subjects experienced regret when the outcome of the alternative choice was revealed, as compared to when it was not revealed. This experience of regret led subjects to adapt their behavior towards more regret-averse choices in subsequent gambles. Interestingly, patients with lesions in the orbital frontal cortex (OFC) did not generate a regret response as measured by subjective ratings or skin conductance, nor did they adapt their behavior to select more regret-averse choices in subsequent trials. The authors interpreted these findings to mean that the OFC is associated with counter-factual thinking that is crucial to the experience of regret.

In a subsequent study using fMRI, Coricelli et al. (2005) examined the brain response associated with both anticipated and experienced regret in healthy subjects. The authors parametrically manipulated experienced regret and observed an increase in activity in the MOFC, DACC, and hippocampus. This pattern of activity was distinct from outcome evaluation and experienced disappointment. Further, the authors noted that during the course of the experiment, the subjects became increasingly regret-averse.

These findings suggest that expected emotions, such as regret, can influence decision-making behavior, and are also associated with a specific neural substrate. The experience of regret seems to be associated with the MOFC, which may potentially be processing the counterfactual thinking associated with the emotion. Future research needs to experimentally tease apart exactly what aspect of regret is associated with the MOFC. Nonetheless, the behavioral evidence from the lesion patients and the neuroimaging results provides converging evidence that the MOFC is critical in the experience of this emotion, and that this in turn influences decision-making.

NEURAL EVIDENCE OF IMMEDIATE EMOTIONS

Immediate emotional reactions to a set of potential choices can also impact the decision-making process. Broadly, this has been termed the "affect heuristic" and it can occur automatically with or without conscious awareness (Slovic et al., 2002). These emotions may be associated with brain regions that automatically process information pertaining to somatic states that can lead to arousal, which in turn simultaneously signal other physiological responses and higher-order processing. These regions appear to be involved in processing of alternatives at an earlier stage as compared to expected emotions, which are more cognitive (top down) in nature. Candidate regions involved in the processing of immediate emotions include the amygdala and insula. The following section will review evidence associated with the neural substrates of immediate emotions in a variety of domains, including uncertainty, social decision-making, and moral decision-making.

Uncertainty

Many experiments have demonstrated people's aversion to uncertainty in the context of decision-making, both in terms of the risk and the ambiguity of decision alternatives. Preliminary neural evidence supports the behavioral results that distinguish between the effects of risk and ambiguity on decision-making, and suggests that ambiguity may be associated with more negative aversive states. The neural computation of expected risk, like that of expected reward, may be localized to the ventral striatum (Fiorillo, Tobler, & Schultz, 2003). However, one study has reported a temporal dissociation, in which ventral striatal activity may be more delayed when calculating expected risk as compared to expected reward (Preuschoff, Bossaerts, & Quartz, 2006).

Ambiguity appears to be associated with even more aversive somatic states. Early conditioning studies in dogs found that unpredictable shocks lead to a state of learned helplessness (Seligman & Maier, 1967). In fear conditioning studies with humans, people are willing to withstand stronger electric shocks if they are more predictable than weaker, uncertain ones (Berns et al., 2006). Research investigating the neural substrates of ambiguity has implicated the insula, DLPFC, posterior parietal regions (Huettel, Stowe, Gordon, Warner, & Platt, 2006), amygdala and LOFC (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005). This provides further evidence that unpredictability is associated with a negative somato-visceral state. In addition, similar to regret (Camille et al., 2004), damage to the OFC appears to lead to decreased risk and ambiguity aversion (Hsu et al., 2005).

Social Decision-Making

Immediate emotions have also been found to influence decision-making in social contexts. An economic game commonly used to study emotional processing in social situations is the Ultimatum Game (Guth, Schmittberger, & Schwarze, 1982). This game is typically played with two players — a proposer and a responder. The proposer is charged with splitting a sum of money between the two players. This split can range from fair ("We each get an equal share") to unfair ("You get nothing"). The responder must either accept or reject the offer put forth by the proposer. If the responder accepts the offer, each player is paid according to what is proposed by the proposer. If the responder rejects the offer, however, neither player receives anything. The standard game theoretic solution is for the proposer to offer the least amount of money that they believe the responder will accept. The responder should accept any offer greater than zero, on the grounds that something is better than nothing. However, many experiments have demonstrated that proposers typically offer about half of the money, and that responders reject offers of 20% of the pot or less about 50% of the time (Camerer, 2003).

Some empirical evidence has demonstrated that emotional reactions to unfairness, such as anger, underlie responder rejections (Pillutla & Murnighan, 1996; Xiao & Houser, 2005). These emotional reactions that lead to the rejection of unfair offers may be related to a fundamental evolutionary adaptive mechanism that serves to form and maintain social norms and reputation (Nowak, Page, & Sigmund, 2000).

Our group has investigated the neural systems involved in playing the ultimatum game. Sanfey et al. (2003) scanned subjects playing a one-shot ultimatum game in the role of a responder using fMRI. The subjects played with multiple human opponents and also with a computer opponent, which served as a control condition. In the comparison between unfair and fair offers, the authors observed an increase in activation in the bilateral anterior insula, DLPFC, and ACC. There was also a significant interaction in the bilateral insula between opponent type and fairness of the offer, with the activation greatest in the human unfair offers. Activity in the insula also correlated with the likelihood of rejecting an offer. Further, we found increased DLPFC activation in relation to an unfair offer, which we proposed reflects the increased cognitive demands needed to overcome the negative emotional response to an unfair offer. While this study provided a useful initial examination of how the brain makes decisions in a social context, many questions remain.

One question remaining is whether the subjects actually experienced a negative emotional reaction to unfair offers. To address this question, van 't Wout, Kahn, Sanfey, & Aleman (2006) measured electrodermal activity to assess the level of autonomic arousal experienced during the ultimatum game. Electrodermal activity has previously been found to be associated with insula activity (Critchley et al., 2000). Consistent with these findings, the authors observed increased electrodermal activity during unfair offers compared to fair offers. This activity was in turn associated with rejection of offers. Similar to the original Sanfey et al. (2003) study, this effect was specific to trials with human opponents. Subjects did not generate an electrodermal response to the computer control trials.

Another question is whether the DLPFC response to unfair offers was actually the result of maintaining a deliberative goal. To address this question, van 't Wout, Kahn, Sanfey, & Aleman (2005) used repetitive transcranial magnetic stimulation (rTMS) to stimulate activity in the right DLPFC. This noninvasive technique allows for the temporary manipulation of neural activity by delivering a series of short bursts of magnetic pulses using a magnetic wand (Walsh & Pacual-Leone, 2003). The results were consistent with the prediction. Compared to sham stimulation (coil positioned but no pulse delivered), rTMS applied to the right DLPFC led to an increase in acceptances of unfair offers. This finding has recently been replicated by another group (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006), though their interpretation differs somewhat.

Finally, in order to investigate the proposed role of the insula, we used simple emotional primes, namely movie clips, to elicit mood changes prior to playing the Ultimatum game. Based on the fMRI study outlined above, we hypothesized that negative emotion states would lead to increased insula activity, and thereby decrease acceptance rates of unfair offers. This is indeed what was observed, with acceptance rates while in a sad mood being significantly reduced as compared to both neutral and happy moods (Harle & Sanfey, 2007).

Recently, Koenigs and Tranel (2007) compared the performance of patients with VMPFC damage to healthy controls on the ultimatum game. They found that patients with VMPFC damage rejected more unfair offers compared to control subjects. At face value, this finding might contradict the hypothesis that patients with VMPFC damage should generate less immediate emotions to an unfair offer and therefore act in a more economically rational fashion. However, previous imaging results suggest that the emotional response to an unfair offer might be associated more with the insula (Sanfey et al., 2003). Further, there is some evidence that the

MOFC might provide inhibitory control of limbic regions such as the insula and amygdala (Critchley, Melmed, Featherstone, Mathias, & Dolan, 2001; Phelps, Delgado, Nearing, & LeDoux, 2004). Therefore, a VMPFC lesion would disinhibit the insula and lead to an increased emotional response and potentially higher rejection rates. This inability to regulate emotions is a common symptom of VMPFC damage (which typically includes the VACC) and has been well described (Bechara et al., 2000; Drevets, 2007; Rolls, Hornak, Wade, & McGrath, 1994).

Moral Decision-Making

In the domain of moral psychology, psychologists and philosophers have recently made the distinction between moral intuition and moral reasoning (Haidt, 2007). Similar to other dual-process models discussed above, moral intuition has been described as a fast, automatic emotional system. Moral reasoning has been described as more slow, deliberative, and cognitive. Greene et al. (2001) conducted a study investigating the neural correlates of moral intuition, in which subjects were presented with a number of moral dilemmas that had previously been rated as either moral-personal, moral-impersonal, or non-moral.

The authors hypothesized that moral-personal dilemmas should be the most emotionally engaging, and therefore associated with greater activity in brain regions involved with emotion processing. In support of their hypotheses, the authors observed increased activity in the MPFC, posterior cingulate cortex (PCC), and bilateral superior temporal sulci while making the moral-personal decisions. In a follow-up study, the authors replicated their previous findings and observed increased activity in the DACC and DLPFC in trials where utilitarian decisions required violating personal morals, which was hypothesized to reflect increased conflict between emotional and cognitive systems. In these high emotional conflict trials, the authors also observed increased activity in the anterior insula and PCC. The authors proposed that the DLPFC is involved in making utilitarian judgments.

In support of this hypothesis, other investigators have found that patients with damage to the VMPFC endorsed more utilitarian moral judgments than either healthy controls or patients with lesions to other regions (Koenigs et al., 2007). This supports the notion that the VMPFC is necessary for generating emotional responses to moral-personal dilemmas. Patients with VMPFC lesions do not generate an emotional response to the

moral-personal dilemmas and thus do not generate the conflict response described by Greene, Nystrom, Engell, Darley, and Cohen (2004). This potentially explains the increase in the endorsement of utilitarian judgments. In summary, these findings suggest that brain regions associated with emotion, such as the medial PFC, insula, and PCC, process the quick emotional responses to moral judgments, while the DLPFC may be involved in formulating more deliberative utilitarian judgments. These two systems may be arbitrated by the DACC conflict system.

DISCUSSION

The goal of neuroeconomics is to provide novel insights into processes underlying judgment and decision-making. Previous behavioral research has emphasized the importance of emotions in this process (Damasio, 1994; Loewenstein & Lerner, 2003; Loewenstein et al., 2001; Mellers et al., 1999; Slovic et al., 2002). We have attempted to present evidence that illustrates the potential neural substrates mediating emotional influences on decision-making. While the work reviewed here is preliminary in nature, there is growing evidence for a distinction between expected emotions and immediate emotions. Immediate emotions seem to be associated with more bottom-up automatic responses consistent with conceptualizations of the function of the amygdala and insula. Expected emotions, in contrast, appear to involve more top-down responses associated with regions such as the MOFC, which are important in assigning value and evaluating outcomes.

Other regions associated with higher-order cognitive functions, such as maintaining and manipulating information and goal states and response selection and control, may be linked to more dorsal PFC regions like the DLPFC and DACC (Carter et al., 2000; Miller & Cohen, 2001). Taken together, these findings suggest a neural dissociation between regions associated with automatic and controlled processing. An interesting avenue for future research would be to investigate how these systems cooperate and compete, and how this arbitration signal is generated in the brain (Daw, Niv, & Dayan, 2005). Preliminary evidence suggests that this function may be located in the DACC (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 2000), with some studies illustrating that this conflict might be observed when emotional responses contradict higher-order goal states, such as maintaining reputation, making money, or evaluating a moral dilemma (Greene et al., 2004; Sanfey et al., 2003).

In interpreting these findings, it is important to note some further caveats and limitations. First, emotion is a notoriously nebulous construct and to this day there is some disagreement about what actually constitutes an emotional state. Given the difficulty in defining this concept, it should come as no surprise that it is also difficult to measure. Emotion is typically measured using either subjective ratings or physiological measures. Unfortunately, there is conflicting evidence that these two measures are even related (for a discussion of the methods in emotion research see Coan & Allen, 2007). Additionally, a common approach within the field of neuroimaging is to observe a pattern of activation correlated with a behavioral measure, and then to use the "reverse inference" to assume that this pattern of activity necessitates the presence of this function (Poldrack, 2006). For example, repeated observation of amygdala activity in conjunction with the experience of fear does not necessarily mean that any activation of this structure *requires* that a fear response was present.

Finally, it is important to note that the theory of multiple systems remains somewhat controversial. Others have argued that "there is no neurobiological evidence that emotional and non-emotional systems are fully distinct in the architecture of the primate brain" (Glimcher et al., 2005), and indeed, the fact that all regions of the brain presumably serve multiple functions thus implies that there can never be fully dissociable emotional and cognitive regions. This criticism of the more extreme modularity view is likely true; however, the evidence discussed above does suggest that certain functions and processes may be subserved by different, probably overlapping, subsystems. Innovative multivariate statistical methods are beginning to facilitate the investigation of these systems-level networks (Damoiseaux et al., 2006; Fox et al., 2005; Greicius, Krasnow, Reiss, & Menon, 2003).

In summary, we have reviewed recent findings from the emerging field of neuroeconomics that have examined emotional influences on decision-making. These findings seem to be consistent with previous behavioral conceptualizations of emotional influences on behavior, which differentiate between expected and immediate emotions. We have also briefly discussed how emotion might fit into a dual-process framework, though it should be noted that the complex system-level dynamics of the brain most likely require a more refined and detailed theoretical framework. Nonetheless, even using this approach, we can make finer-grained distinctions between types of emotions, each of which appear to have dissociable neural substrates. Further development of this research direction, in conjunction with progress in both the theoretical and empirical understanding of emotion and techniques for better specification of neural activation, offers an exciting prospect for better understanding how our decisions are affected, for good and ill, by our emotions.

REFERENCES

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature, 372*(6507), 669-672.

Aggleton, J. (Ed.) (1992). *The amygdala.* New York: Wiley-Liss.

Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience, 6*(2), 115-116.

Baker, S. C., Frith, C. D., Frackowiak, R. S., & Dolan, R. J. (1996). Active representation of shape and spatial location in man. *Cerebral Cortex, 6*(4), 612-619.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex, 10*(3), 295-307.

Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science, 275*(5304), 1293-1295.

Bell, D. E. (1982). Regret in decision making under uncertainty. *Operations Research, 33*, 1-27.

Bell, D. E. (1985). Disappointment in decision making under uncertainty. *Operations Research, 33*, 1-27.

Berns, G. S., Chappelow, J., Cekic, M., Zink, C. F., Pagnoni, G., & Martin-Skurski, M. E. (2006). Neurobiological substrates of dread. *Science, 312*(5774), 754-758.

Blumenthal, A. (1980). A Wundt primer: The operating characteristics of consciousness. In: R. Rieber & D. Robinson (Eds), *Wilhelm Wundt in historical perspective* (pp. 121-144). New York: Plenum.

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature, 402*(6758), 179-181.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4*(6), 215-222.

Byrne, R. M. (2002). Mental models and counterfactual thoughts about what might have been. *Trends in Cognitive Sciences, 6*(10), 426-431.

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience, 3*(11), 1077-1078.

Calder, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience, 2*(5), 352-363.

Camerer, C. F. (2003). Dictator, ultimatum, and trust games. In: C. F. Camerer (Ed.), *Behavioral game theory* (pp. 43-116). New York: Russell Sage Foundation.

Camille, N., Coricelli, G., Sallet, J., Pradat-Diehl, P., Duhamel, J. R., & Sirigu, A. (2004). The involvement of the orbitofrontal cortex in the experience of regret. *Science, 304*(5674), 1167-1170.

Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science, 280*(5364), 747-749.

Carter, C. S., Macdonald, A. M., Botvinick, M., Ross, L. L., Stenger, V. A., Noll, D., & Cohen, J. D. (2000). Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 97*(4), 1944-1948.

Chaiken, S., & Trope, Y. (1999). *Dual process theories in social psychology*. New York: The Guilford Press.

Coan, J. A., & Allen, J. B. (Eds) (2007). *Handbook of emotion elicitation and assessment*. New York, NY: Oxford University Press.

Coricelli, G., Critchley, H. D., Joffily, M., O'Doherty, J. P., Sirigu, A., & Dolan, R. J. (2005). Regret and its avoidance: A neuroimaging study of choice behavior. *Nature Neuroscience, 8*(9), 1255-1262.

Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience, 3*(8), 655-666.

Critchley, H. D., Elliott, R., Mathias, C. J., & Dolan, R. J. (2000). Neural activity relating to generation and representation of galvanic skin conductance responses: A functional magnetic resonance imaging study. *Journal of Neuroscience, 20*(8), 3033-3040.

Critchley, H. D., Mathias, C. J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B. K., Cipolotti, L., Shallice, T., & Dolan, R. J. (2003). Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. *Brain, 126*(Pt 10), 2139-2152.

Critchley, H. D., Melmed, R. N., Featherstone, E., Mathias, C. J., & Dolan, R. J. (2001). Brain activity during biofeedback relaxation: A functional neuroimaging investigation. *Brain, 124*(Pt 5), 1003-1012.

Damasio, A. R. (1994). *Descartes' error: Emotion, reason, and the human brain*. New York: Penguin Putnam.

Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L., Parvizi, J., & Hichwa, R. D. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience, 3*, 1049-1056.

Damoiseaux, J. S., Rombouts, S. A., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., & Beckmann, C. F. (2006). Consistent resting-state networks across healthy subjects. *PNAS, 103*(37), 13848-13853.

Davidson, R. J. (1995). Cerebral asymmetry, emotion, and affective style. In: R. J. Davidson & K. Hughdal (Eds), *Brain asymmetry* (pp. 361-387). Cambridge: MIT Press.

Daw, N. D., Niv, Y., & Dayan, P. (2005). Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nature Neuroscience, 8*(12), 1704-1711.

Descartes, R. (1664). *L'Homme (Treatise on Man)*. (T. S. Hall, Trans.). Cambridge, MA: Harvard University Press.

Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain, 118*(Pt 1), 279-306.

Drevets, W. C. (1999). Prefrontal cortical-amygdalar metabolism in major depression. *Annals of the New York Academy of Sciences, 877*, 614-637.

Drevets, W. C. (2007). Orbitofrontal cortex function and structure in depression. *Annals of the New York Academy of Sciences*.

Duchenne, G. B. A. (1862). *Mecanisme de la Physionomie Humaine, ou Analyse Electro-Physiologique de l'Expression des Passions Applicable a la Pratique des Arts Plastiques*. Paris: J.B. Balliere.

Dunn, L. T., & Everitt, B. J. (1988). Double dissociations of the effects of amygdala and insular cortex lesions on conditioned taste aversion, passive avoidance, and neophobia in the rat using the excitotoxin ibotenic acid. *Behavioral Neuroscience, 102*(1), 3-23.

Epstein, S. (1994). Integration of the cognitive and the psychodynamic unconscious. *American Psychologist, 49*(8), 709-724.

Evans, J. S. B. T., & Over, D. E. (1996). *Rationality and reasoning*. Hove, East Sussex, UK: Psychology Press.

Fiorillo, C. D., Tobler, P. N., & Schultz, W. (2003). Discrete coding of reward probability and uncertainty by dopamine neurons. *Science, 299*(5614), 1898-1902.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America, 102*(27), 9673-9678.

Garavan, H., Ross, T. J., Murphy, K., Roche, R. A., & Stein, E. A. (2002). Dissociable executive functions in the dynamic control of behavior: Inhibition, error detection, and correction. *Neuroimage, 17*(4), 1820-1829.

Glimcher, P. W., Dorris, M. C., & Bayer, H. M. (2005). Physiological utility theory and the neuroeconomics of choice. *Games and Economic Behavior, 52*(2), 213-256.

Glimcher, P. W., & Rustichini, A. (2004). Neuroeconomics: The consilience of brain and decision. *Science, 306*(5695), 447-452.

Gottfried, J. A., O'Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science, 301*(5636), 1104-1107.

Greene, J. D., Nystrom, L. E., Engell, A. D., Darley, J. M., & Cohen, J. D. (2004). The neural bases of cognitive conflict and control in moral judgment. *Neuron, 44*(2), 389-400.

Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M., & Cohen, J. D. (2001). An fMRI investigation of emotional engagement in moral judgment. *Science, 293*(5537), 2105-2108.

Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences of the United States of America, 100*(1), 253-258.

Guth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization, 3*, 367.

Haidt, J. (2001). The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychological Review, 108*(4), 814-834.

Haidt, J. (2007). The new synthesis in moral psychology. *Science, 316*(5827), 998-1002.

Hammond, K. R. (2000). *Judgment under stress*. New York: Oxford University Press.

Harle, K., & Sanfey, A. G. (2007). Incidental sadness biases social economic decisions in the ultimatum game. *Emotion, 7*(4), 876-881.

Holstege, G. (2002). Emotional innervation of facial musculature. *Movement Disorders, 17*(Suppl 2), S12-S16.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., & Camerer, C. F. (2005). Neural systems responding to degrees of uncertainty in human decision-making. *Science, 310*(5754), 1680-1683.

Huettel, S. A., Stowe, C. J., Gordon, E. M., Warner, B. T., & Platt, M. L. (2006). Neural signatures of economic preferences for risk and ambiguity. *Neuron, 49*(5), 765-775.

Isen, A. M. (2000). Positive affect and decision making. In: M. Lewis & J. M. Haviland-Jones (Eds). *Handbook of emotions* (pp. 417-435). New York: Guilford Press.

Isenberg, N., Silbersweig, D., Engelien, A., Emmerich, S., Malavade, K., Beattie, B., Leon, A. C., & Stern, E. (1999). Linguistic threat activates the human amygdala. *Proceedings of the National Academy of Sciences of the United States of America, 96*(18), 10456-10459.

James, W. (1884). What is an emotion? *Mind, 9,* 188-205.

James, W. (1890). *The principles of psychology.* New York: Henry Holt and Co.

Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologist, 58*(9), 697-720.

Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V., & Fehr, E. (2006). Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science, 314*(5800), 829-832.

Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience, 21*(16), RC159.

Knutson, B., Fong, G. W., Bennett, S. M., Adams, C. M., & Hommer, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: Characterization with rapid event-related fMRI. *Neuroimage, 18*(2), 263-272.

Koenigs, M., & Tranel, D. (2007). Irrational economic decision-making after ventromedial prefrontal damage: Evidence from the Ultimatum Game. *Journal of Neuroscience, 27*(4), 951-956.

Koenigs, M., Young, L., Adolphs, R., Tranel, D., Cushman, F., Hauser, M., & Damasio, A. (2007). Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature, 446*(7138), 908-911.

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience, 7*(1), 54-64.

Lane, R. D. (2000). Neural correlates of conscious emotional experience. In: R. D. Lane & L. Nadel (Eds). *Cognitive neuroscience of emotion* (pp. 345-370). New York: Oxford University Press.

Lange, C. S. (1887). Ueber Gemuthsbewegungen, *3, 8.*

Lazarus, R. S. (1982). Thoughts on the relations between emotion and cognition. *American Psychologist, 37*(9), 1019-1024.

Ledoux, J. (1996). *The emotional brain.* New York: Simon & Schuster.

Lerner, J. S., Small, D. A., & Loewenstein, G. (2004). Heart strings and purse strings: Carryover effects of emotions on economic decisions. *Psychological Science, 15*(5), 337-341.

Loewenstein, G., & Lerner, J. S. (2003). The role of affect in decision making. In: R. J. Davidson, K. R. Scherer & H. H. Goldsmith (Eds), *Handbook of affective sciences.* New York, NY: Oxford University Press.

Loewenstein, G. F., Weber, E. U., Hsee, C. K., & Welch, N. (2001). Risk as feelings. *Psychological Bulletin, 127*(2), 267-286.

Loomes, G., & Sugden, R. (1982). Regret theory: An alternative of rational choice under uncertainty. *Economic Journal, 92,* 805-824.

Loomes, G., & Sugden, R. (1986). Disappointment and dynamic consistency in choice under uncertainty. *Review of Economic Studies, 53,* 271-282.

Mayberg, H. S., Lozano, A. M., Voon, V., McNeely, H. E., Seminowicz, D., Hamani, C., Schwalb, J. M., & Kennedy, S. H. (2005). Deep brain stimulation for treatment-resistant depression. *Neuron, 45*(5), 651-660.

McCabe, K., Houser, D., Ryan, L., Smith, V., & Trouard, T. (2001). A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Sciences of the United States of America, 98*(20), 11832-11835.

McClure, S. M., Laibson, D. L., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science, 306*(5695), 503-507.

McKay, L. C., Evans, K. C., Frackowiak, R. S., & Corfield, D. R. (2003). Neural correlates of voluntary breathing in humans. *Journal of Applied Physiology, 95*(3), 1170-1178.

Mellers, B., Schwartz, A., & Ritov, I. (1997). Elation and disappointment: Emotional responses to risky options. *Psychological Science, 8,* 423-429.

Mellers, B., Schwatz, A., & Ritov, I. (1999). Emotion-based choice. *Journal of Experimental Psychology, 128*(3), 332-345.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24,* 167-202.

Moll, J., de Oliveira-Souza, R., Moll, F. T., Ignacio, F. A., Bramati, I. E., Caparelli-Daquer, E. M., & Eslinger, P. J. (2005). The moral affiliations of disgust: A functional MRI study. *Cognitive and Behavioral Neurology, 18*(1), 68-78.

Montague, P. R., King-Casas, B., & Cohen, J. D. (2006). Imaging valuation models in human choice. *Annual Review of Neuroscience, 29,* 417-448.

Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain, 121*(Pt 1), 47-57.

Naqvi, N. H., Rudrauf, D., Damasio, H., & Bechara, A. (2007). Damage to the insula disrupts addiction to cigarette smoking. *Science, 315*(5811), 531-534.

Nolte, J. (2002). *The human brain: An introduction to its functional anatomy.* St. Louis, MO: Mosby.

Nowak, M. A., Page, K. M., & Sigmund, K. (2000). Fairness versus reason in the ultimatum game. *Science, 289*(5485), 1773-1775.

O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., & Dolan, R. J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science, 304*(5669), 452-454.

O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neuroscience, 4*(1), 95-102.

O'Doherty, J. P., Hampton, A., & Kim, H. (2007). Model-based fMRI and its application to reward learning and decision making. *Annals of the New York Academy of Sciences, 1104,* 35-53.

Penfield, W., & Faulk, M. E., Jr. (1955). The insula: further observations on its function. *Brain, 78*(4), 445-470.

Phelps, E. A., Delgado, M. R., Nearing, K. I., & LeDoux, J. E. (2004). Extinction learning in humans: Role of the amygdala and vmPFC. *Neuron, 43*(6), 897-905.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48*(2), 175-187.

Phillips, M. L., Drevets, W. C., Rauch, S. L., & Lane, R. (2003). Neurobiology of emotion perception I: The neural basis of normal emotion perception. *Biological Psychiatry, 54*(5), 504-514.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., & Williams, S. C. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature, 389*(6650), 495-498.

Pillutla, M. M., & Murnighan, J. K. (1996). Unfairness, anger, and spite: Emotional rejection of ultimatum offers. *Organizational Behavior and Human Decision Processes, 68,* 208.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences, 10*(2), 59 63.

Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: Converging evidence from animal and human brain studies. *Neuropsychologia, 41*(3), 245 251.

Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neurosciences, 17*(2), 75 79.

Preuschoff, K., Bossaerts, P., & Quartz, S. R. (2006). Neural differentiation of expected reward and risk in human subcortical structures. *Neuron, 51*(3), 381 390.

Rolls, E. T., Hornak, J., Wade, D., & McGrath, J. (1994). Emotion-related learning in patients with social and emotional changes associated with frontal lobe damage. *Journal of Neurology, Neurosurgery, and Psychiatry, 57*(12), 1518 1524.

Sanfey, A. G., & Chang, L. J. (2008). Multiple systems in decision-making. In: W. T. Tucker, S. Ferson, A. Finkel, T. F. Long, D. Slavin & P. Wright (Eds.), *Strategies for risk communication: Evolution, evidence, experience.* New York: Annals of the New York Academy of Sciences.

Sanfey, A. G., Loewenstein, G., McClure, S. M., & Cohen, J. D. (2006). Neuroeconomics: Cross-currents in research on decision-making. *Trends in Cognitive Sciences, 10*(3), 108 116.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science, 300*(5626), 1755 1758.

Schachter, S., & Singer, J. E. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychological Review, 69,* 379 399.

Schneider, W., & Chein, J. M. (2003). Controlled & automatic processing: Behavior, theory, and biological mechanisms. *Cognitive Science, 27,* 525 559.

Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. detection, search, attention. *Psychological Review, 84*(1), 1 66.

Schwarz, N. (2000). Emotion, cognition, and decision-making. *Cognition and Emotion, 14*(4), 433 440.

Seligman, M. E., & Maier, S. F. (1967). Failure to escape traumatic shock. *Journal of Experimental Psychology, 74*(1), 1 9.

Sloman, S. (1996). The empirical case for two systems of reasoning. *Psychological Bulletin, 119*(1), 3 22.

Slovic, P., Finucane, M. L., Peters, E., & MacGregor, D. G. (2002). The affect heuristic. In: T. Gilovich, D. Griffin & D. Kahneman (Eds.), *Heuristics and biases* (pp. 397 420). New York: Cambridge University Press.

Small, D. M., Zald, D. H., Jones-Gotman, M., Zatorre, R. J., Pardo, J. V., Frey, S., & Petrides, M. (1999). Human cortical gustatory areas: A review of functional neuroimaging data. *Neuroreport, 10*(1), 7 14.

Stanovich, K. E., & West, R. F. (2000). Individual differences in reasoning: Implications for the rationality debate? *Behavioral and Brain Functions, 23,* 645 726.

Sugrue, L. P., Corrado, G. S., & Newsome, W. T. (2005). Choosing the greater of two goods: Neural currencies for valuation and decision making. *Nature Reviews Neuroscience, 6*(5), 363 375.

Trosch, R. M., Sze, G., Brass, L. M., & Waxman, S. G. (1990). Emotional facial paresis with striatocapsular infarction. *Journal of the Neurological Sciences, 98*(2 3), 195 201.

van't Wout, M., Kahn, R. S., Sanfey, A. G., & Aleman, A. (2005). Repetitive transcranial magnetic stimulation over the right dorsolateral prefrontal cortex affects strategic decision-making. *Cognitive Neuroscience and Neuropsychology, 16*(16), 1849 1852.

van't Wout, M., Kahn, R. S., Sanfey, A. G., & Aleman, A. (2006). Affective state and decision-making in the Ultimatum Game. *Experimental Brain Research, 169*(4), 564 568.

Walsh, V., & Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: A neuro-chronometrics of mind.* Cambridge, MA: MIT Press.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18*(1), 411 418.

Xiao, E., & Houser, D. (2005). Emotion expression in human punishment behavior. *Proceedings of the National Academy of Sciences of the United States of America, 102*(20), 7398 7401.

Yechiam, E., Busemeyer, J. R., Stout, J. C., & Bechara, A. (2005). Using cognitive models to map relations between neuropsychological disorders and human decision-making deficits. *Psychological Science, 16*(12), 973 978.

Zeelenberg, M., Beattie, J., van der Pligt, J., & de Vries, N. (1996). Consequences of regret aversion: Effects of expected feedback on risky decision making. *Organizational Behavior and Human Decision Processes, 65,* 148 158.

Zeki, S. (1993). *A vision of the brain.* London: Blackwell.