Emotion and Decision Making: Multiple Modulatory Neural Circuits

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Abstract

Although the prevalent view of emotion and decision making is derived from the notion that there are dual systems of emotion and reason, a modulatory relationship more accurately reflects the current research in affective neuroscience and neuroeconomics. Studies show two potential mechanisms for affect's modulation of the computation of subjective value and decisions. Incidental affective states may carry over to the assessment of subjective value and the decision, and emotional reactions to the choice may be incorporated into the value calculation. In addition, this modulatory relationship is reciprocal: Changing emotion can change choices. This research suggests that the neural mechanisms mediating the relation between affect and choice vary depending on which affective component is engaged and which decision variables are assessed. We suggest that a detailed and nuanced understanding of emotion and decision making requires characterizing the multiple modulatory neural circuits underlying the different means by which emotion and affect can influence choices.

Contents

BEYOND DUAL SYSTEMS IN THE MIND AND BRAIN: A MODULATORY ROLE FOR EMOTION IN DECISION MAKING

The prevalent view of the role of emotion in decision making in economics, psychology, and, more recently, neuroscience is the dual systems approach. In economics, choices have been characterized as relying on either System 1 or System 2, with emotion as one of the factors contributing to the more automatic, less deliberative system 1 (Kahneman 2011). In psychology, the terms "hot" versus "cool" have been used to describe decisions driven by affect or not (e.g., Figner et al. 2009; see sidebar, Dual-Process Theories). In neuroscience, brain-imaging research has been used to argue that the human mind is "vulcanized" such that our highly developed prefrontal cortex can be used to overcome the emotional or limbic responses that may sway us to perform irrationally (Cohen 2005). These modern dual-system accounts of the relation between emotion and decision making have a long history. The idea that opposing forces of emotion and reason compete in the human mind is prevalent in Western thought, highlighted by a range of scholars including philosophers such as Plato and Kant and the father of psychoanalysis, Sigmund Freud (Peters 1970). The intuitive nature of this distinction is also apparent in the everyday language used when reflecting on decisions as being made with the heart or the head.

The notion that there are distinct systems for emotion and cognition was also apparent in early theories of brain anatomy. Building on earlier work by Paul Broca and James Papez, Paul Maclean introduced the term "limbic system" in 1952 to describe the phylogenetically older brain regions that lined the inner border of the cortex that he proposed were responsible for basic emotional responses (Lambert 2003) (see **Figure 1*a***). The limbic system quickly became known as the emotional center of the brain, with the neocortex underlying higher cognitive functions, including reason. This early theory was highly influential in its time; however, as basic research into neuroanatomy and structure-function relationships progressed over the past several decades, the limbic system concept did not hold up. For example, a region of the neocortex,

DUAL-PROCESS THEORIES

Dual-process theories are a dominant class of theories of human decision making that argue for the existence of two separate, opposing decision systems. Choice results from competition between these two systems: One is generally emotional, fast, automatic, "hot," and/or subconscious, whereas the other is cognitive, slow, deliberative, "cool," and/or explicit. Some specific theories using this structure include the following.

- System 1/System 2: Emotion is considered part of System 1, which "operates automatically and quickly, with little or no effort and no sense of voluntary control. System 2 allocates attention to the effortful mental activities that demand it, including complex computations. The operations of System 2 are often associated with the subjective experience of agency, choice, and concentration" (Kahneman 2011, pp. 20–21).
- Hot/cool: In this theory, positing a hot emotional system and a cool cognitive system, "risk taking [is] the result of a competition between two neural systems. . .Affective processing is spontaneous and automatic, operates by principles of similarity and contiguity, and influences behavior by affective impulses. . . . The cognitive-control system . . . is the neural basis of deliberative processing, which is effortful, controlled, and operates according to formal rules of logic . . . [and] it is the neural basis of inhibitory control, a mechanism that can block affective impulses and therefore enables deliberative decision making even in affect-charged situations" (Figner et al. 2009, p. 710).

the orbitofrontal cortex, is important in emotion (Damasio 2005), and the hippocampus, a key component of the limbic system, is critical for the basic cognitive function of memory (Squire 2004). Some researchers have tried to modify the limbic system concept to more accurately reflect the emotion/cognition division (e.g., Cohen 2005, Rolls 2013) (see **Figure 1*b***). However, as our understanding of both the complexity of emotion and its underlying neural systems expands, there is clearly no clean delineation between brain regions underlying emotion and cognition. There is no clear evidence for a unified system that drives emotion. Thus affective neuroscientists and neuroanatomists have suggested that the limbic system concept is no longer useful and should be abandoned to facilitate the development of a more complete and detailed understanding of the representation of emotion in the brain (see LeDoux 2000 for a discussion).

Given that affective neuroscientists now generally view the limbic system concept as obsolete, perhaps it is also time to revisit the usefulness of dual system models to characterize the relation between emotion and decision making. Without a clear instantiation of an emotion system in the brain, it is difficult to conceive of a psychological model that relies on such a system. The importance of neural instantiations for psychological theories has become increasingly apparent as the discipline of cognitive neuroscience evolves. When examining other cognitive functions, such as memory, attention, and perception, a more fine-grained analysis of specific brain circuitries underlying the relation between factors indicative of emotion and those of cognition has emerged. This research suggests a modulatory role for emotion's influence on cognition, and vice versa (see Phelps 2006 for a review). Translating this modulatory view to the study of decision making suggests that affective processes may influence a primary factor underlying choice behavior: the computation of subjective value.

In this review, we explore a range of means by which affective factors may influence choices and highlight investigations of the neural circuitry mediating emotion's modulation of decision making. One challenge in approaching this literature is the recognition that emotion is not a unitary construct, but rather a compilation of component affective processes. Although the precise nature of these component processes is a topic of theoretical debate that goes beyond the scope of this

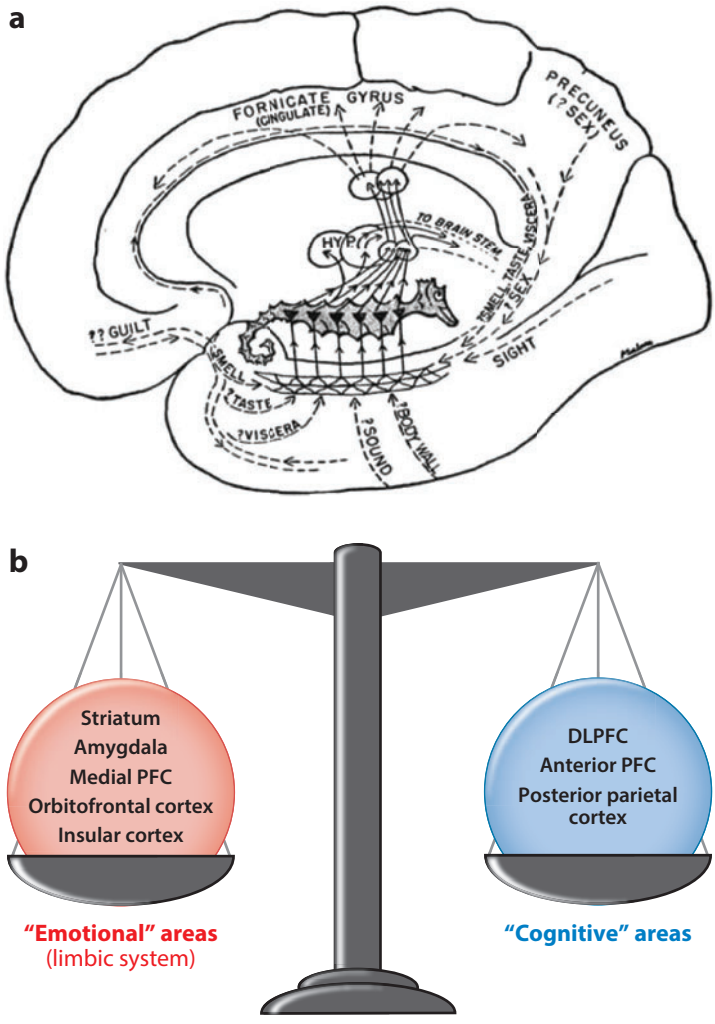

Figure 1

(*a*) The limbic system, centered on the hippocampus, as conceptualized by MacLean (1949). The limbic system concept, as an integrated brain circuit for emotion, has not been supported by more recent neuroanatomical evidence and investigations of brain function (LeDoux 2000). Panel reproduced with permission from Lippincott Williams & Wilkins. (*b*) Dual-process theories of emotion and decision making suggest that choices reflect the outcome of a competition between systems. In this framework, emotional or limbic areas (updated to include other regions; Cohen 2005) are associated with automatic, often irrational choices, whereas cognitive areas are implicated in more deliberative, rational decision making. DLPFC, dorsolateral prefrontal cortex; PFC, prefrontal cortex.

review (e.g., Ekman & Davidson 1994, Scherer 2000, Barrett 2006), a few general distinctions have emerged that will aid in characterizing this literature. The term affect is generally used as the overarching term to describe this collection of component processes, whereas the term emotion refers to a discrete reaction to an internal or external event that can yield a range of synchronized responses, including physiological responses (e.g., flight or fight), facial and/or bodily expressions, subjective feelings, and action tendencies, such as approach or avoid. Although these reactions are synchronized in response to an event, they may not all be present and their intensity can

vary independently. The discrete nature of these emotional reactions is their distinct quality relative to other affective components, although how long they last, from relatively transient to much longer, can vary depending on the nature of the eliciting event and intensity. For the purposes of this review, we differentiate a discrete emotional reaction from a stress response, which is characterized by specific physiological and neurohormonal changes that disrupt homeostasis resulting from a real, imagined, or implied threat (Ulrich-Lai & Herman 2009). The impact of these neurohormonal changes lasts beyond the stressor itself (Dickerson & Kemeny 2004) and induces a relatively lasting affective state. Another lasting affective state is mood, which is defined predominantly by subjective feelings that are not necessarily linked to a specific event. Like emotions, moods can elicit action tendencies. Although these affective processes provide a basis for our characterization of the existing literature on the neural basis of affect and decision making, they do not capture the range of affective experience that may be relevant to understanding decision processes more broadly (see Scherer 2000, 2005 for a more in-depth discussion of component process models of emotion).

One could argue that choice itself is indicative of an affective response because it signals an evaluation of preference, motivation, or subjective value assigned to the choice options. The view that value and emotion are inherently intertwined is more common among psychologists and neuroscientists (e.g., Rolls & Grabenhorst 2008) than economists (e.g., Kahneman 2011), but for this review we focus on evidence that independent affective components modulate the assessment of subjective value and the decision. With this aim in mind, we limit our discussion largely to studies that have explicitly measured and/or manipulated a factor commonly linked to emotion or affect. We do not include studies in which emotion is inferred from choices or blood-oxygenation-level-dependent (BOLD) signal because there is limited evidence of unique BOLD patterns linked to specific affective components (Phelps 2009), a problem commonly known as reverse inference (Poldrack 2006). Given that our primary interest is to characterize the current literature examining the neuroscience of emotion's modulation of decision making, we discuss the growing psychological literature on affect and decision making (Lerner et al. 2015) only if there is also some link to the underlying neural circuitry.

Two broad categories of research explore the modulation of decision making by emotion or affect. The first explores how a decision is altered when it occurs during a specific affective state. In this class of studies, the affective state is incidental to the choice itself but nevertheless modulates the decision. The second class of studies examines how the emotional reaction elicited by the choice itself is incorporated into the computation of subjective value. In the final section, we examine how processes that alter emotion can change choices, highlighting the reciprocal, modulatory relationship between emotion and decision making.

AFFECT CARRYOVER: HOW INCIDENTAL AFFECT MODULATES DECISIONS

One means by which emotion can influence choices is through incidental affect. Incidental affect is a baseline affective state that is unrelated to the decision itself. Studies investigating incidental affect trigger an affective state prior to the decision-making task and evaluate its impact on choices. Below we describe two incidental affective states that have been shown to influence decisions.

Stress

Although stress is a term that is widely used to mean many different things, one clear neurobiological indication of a stress reaction is activation of the hypothalamic-pituitary-adrenal (HPA) axis. Stress reactions are also accompanied by sympathetic nervous system arousal, which can be

more transient, but HPA axis activation results in a cascade of neuroendocrine changes, most notably glucocorticoid release, that can have a relatively lasting impact. These neurohormonal changes influence function in several brain regions implicated in decision making (see Arnsten 2009, Ulrich-Lai & Herman 2009 for reviews) (see **Figure 2*a***).

Several studies examining stress and decision making highlight the impact of stress on the prefrontal cortex (PFC). Even relatively mild stress can impair performance on PFC-dependent tasks, such as working memory, owing to the negative impact of catecholamines and glucocorticoids on PFC function (Arnsten 2009). The impact of stress on other brain regions varies. For example, although mild stress can enhance hippocampal function, more intense and/or prolonged stress impairs the hippocampus (McEwen 2007). In contrast, performance on striatal-dependent tasks is often enhanced with stress (Packard & Goodman 2012), and dopaminergic neurons in the ventral tegmental area and the striatum show transient and lasting stress-specific responses (Ungless et al. 2010). In addition, amygdala function is generally enhanced with stress, and the amygdala modulates some stress effects on the hippocampus, striatum, and PFC (e.g., Roozendaal et al. 2009). Given the uneven effects of stress on the neural circuits that mediate decision making, the impact of stress may vary depending on the intensity and duration of the stressor, as well as on the specific variables assessed in the decision-making task.

The PFC is proposed to play a role in goal-directed decisions, whereas the striatum is generally linked to choices based on habits (Balleine & O'Doherty 2010). To explore this trade-off between PFC- and striatal-mediated choices under stress, Dias-Ferreira and colleagues (2009) examined how chronic stress affected later performance on a devaluation task in rodents. Devaluation tasks assess whether choices are habitual or directed toward a reinforcement goal by altering the value of the reward. If reducing the value of the reward changes behavior, the task is said to be goal directed, whereas if devaluing the reward does not alter behavior, the task is habitual. After training rats to press a lever to receive a food reward, the rats were fed the food to satiety, thus devaluing subsequent reward presentations. Rats who had not been previously stressed reduced their response rate, reflecting the devalued reward outcome. In contrast, stressed rats failed to modify their behavior following devaluation, consistent with habitual responding. Dias-Ferreira et al. (2009) found that chronic, restraint stress resulted in neuronal atrophy of the medial PFC and dorsal medial striatum, a circuit known to be involved in goal-directed actions. They also observed neuronal hypertrophy of the dorsal lateral striatum, a region linked to habit learning.

In humans, it is not possible to experimentally induce chronic stress and observe its long-term consequences, but several techniques have been used to induce acute, mild stress that reliably results in HPA-axis activation (see Dickerson & Kemeny 2004). These acute, mild stressors have been shown to impair performance on PFC-dependent tasks and reduce PFC BOLD responses (e.g., Qin et al. 2009, Raio et al. 2013). Using a devaluation paradigm similar to that described above, Schwabe & Wolf (2009) found that acute stress yields a similar shift from goal-directed to habitual choices in humans. In a follow-up series of studies, Schwabe and colleagues (2010, 2011) administered drugs targeting glucocorticoid and noradrenergic activity to explore the neurohormonal changes that might underlie this stress-induced shift to habitual actions. They observed that administering both hydrocortisone and an α2-adrenoceptor antagonist (yohimbine), which increases noradrenaline levels in the brain, resulted in the shift to habitual actions typically observed with stress, but neither drug alone was sufficient to do so (Schwabe et al. 2010). Conversely, if stressed participants were administered a beta-adrenergic antagonist (propranolol), they failed to demonstrate the typical shift to habitual actions, despite intact increased cortisol with stress (Schwabe et al. 2011). This observation suggests that both glucocorticoids and noradrenaline are necessary neurohormonal components underlying the shift from goal-directed to habitual actions with stress. These findings are consistent with research in nonhuman animals showing that elevated

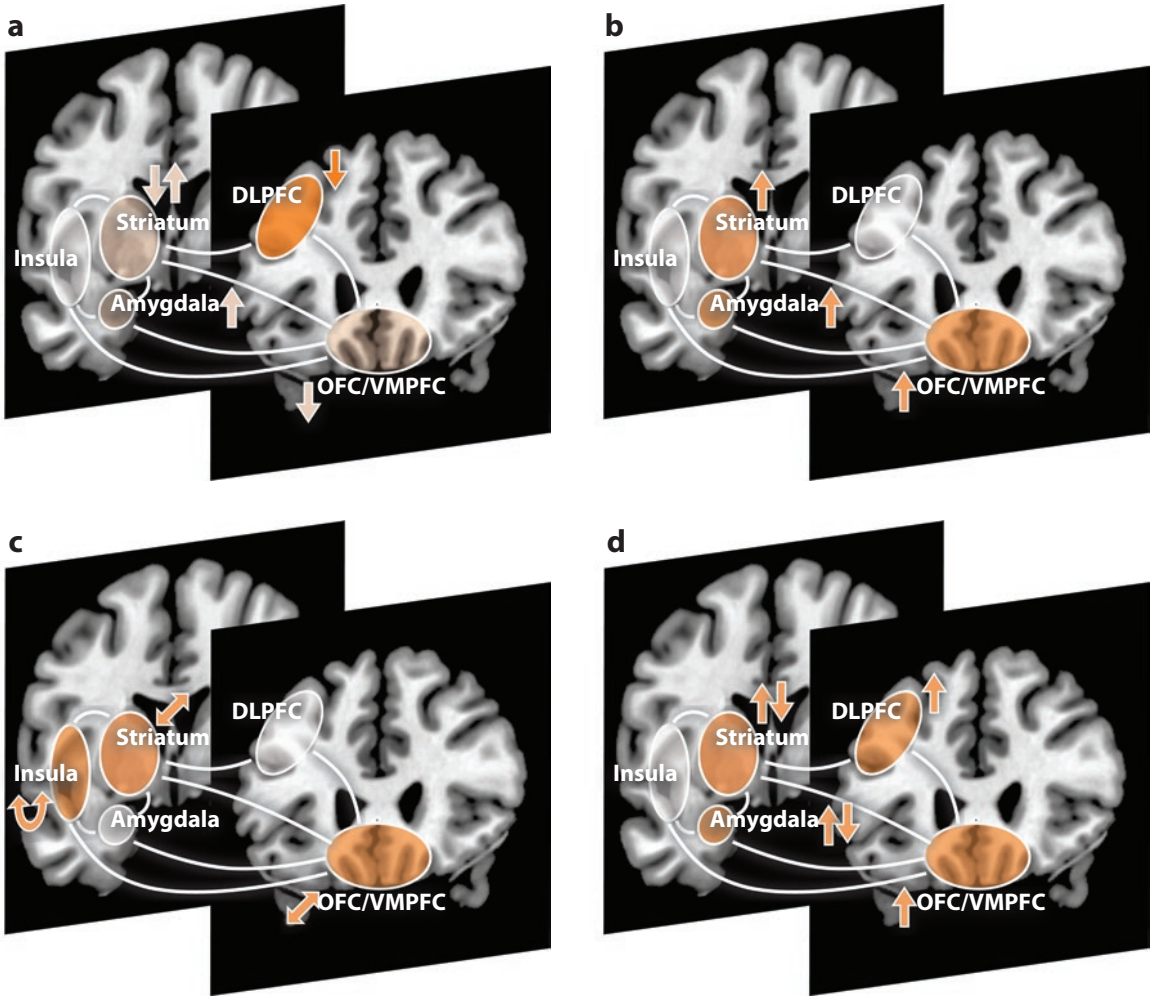

Figure 2

Potential candidates for multiple modulatory neural circuits involved in affect and decision making. (*a*) Decision making under stress. Even mild stress impairs the dorsolateral prefrontal cortex (DLPFC), leading to decreased goal-directed behavior and increased habitual behavior (Schwabe & Wolf 2009, Otto et al. 2013). Stress also impairs the orbitofrontal cortex (OFC)/ventromedial prefrontal cortex (VMPFC) and enhances amygdala function, whereas different subdivisions of the striatum may show increased or decreased reactivity with stress (Arnsten 2009, Roozendaal et al. 2009). (*b*) Emotion contributes to valuation. The amygdala influences the computation of subjective value in the striatum and the OFC/VMPFC and modulates learning from reinforcement (Li et al. 2011, Sokol-Hessner et al. 2012, Rudebeck et al. 2013). (*c*) The relationship between subjective value and BOLD activity. A meta-analysis of fMRI studies (Bartra et al. 2013) shows a linear relationship between subjective value and activity in the OFC/VMPFC and the ventral striatum, whereas the relationship between insula activity and subjective value is U-shaped, suggesting that the insula may contribute to value computation in situations of high arousal or salience. (*d*) Cognitive emotion regulation. The influence of emotion on choice can be altered using cognitive emotion regulation techniques mediated by the DLPFC and VMPFC. Emotional reactions can be increased or decreased with these techniques (Ochsner & Gross 2005), leading to corresponding changes in the amygdala and striatum (Delgado et al. 2008a,b; Sokol-Hessner et al. 2013).

Erratum

noradrenaline levels during stress alter executive control and PFC function, and glucocorticoids play a role in the exaggeration and persistence of this effect. The impact of these neurohormonal changes on the PFC is mediated through the amygdala (Arnsten 2009).

This balance between PFC and striatal contributions to decision making can also be observed in tasks that tap into model-based and model-free reinforcement learning (Daw et al. 2005). In model-free learning, one learns which choice is beneficial through previous experience with its reinforcing consequences, whereas model-based learning requires a model of the environment that allows one to engage in a series of choices that maximize reward. Theoretical models (Daw et al. 2005) and functional magnetic resonance imaging (fMRI) studies (Gläscher et al. 2010) suggest that although both model-based and model-free decisions engage striatal-based reinforcement learning mechanisms, model-based choices also depend on interactions with the lateral PFC. Using a decision-making task that yields different patterns of choices depending on whether one is using a model-free or model-based strategy, Otto and colleagues (2013) found that stress attenuated model-based, but not model-free, contributions to choice behavior. Relatively high baseline working-memory capacity had a protective effect, attenuating the deleterious effect of stress on choices.

Several studies have examined the impact of stress on tasks of risky decision making, although the nature of these findings varies depending on a number of factors. Porcelli & Delgado (2009) found that stress exacerbated the "reflection effect," which is the tendency to be risk seeking when choosing between possible losses and risk averse when choosing between potential gains. However, other risky decision-making tasks have reported that participants are more risk seeking overall under stress (Starcke et al. 2008) or more risk seeking in the loss domain only (Pabst et al. 2013). In addition, the impact of stress on risky decisions may depend on the level of risk (von Helversen & Reiskamp 2013) and may interact with gender (e.g., Preston et al. 2007, Lighthall et al. 2009). As this series of studies indicates, there are likely several decision and individual difference variables that will need to be disentangled to determine how stress may influence different aspects of risky decisions.

The only brain-imaging study on stress and risky decision making to date (Lighthall et al. 2012) used a task in which participants earn points for inflating virtual balloons but must "cash out" before the balloon explodes or risk losing their points. Consistent with earlier findings (Lighthall et al. 2009), this task demonstrated a gender interaction: Males were more risk seeking, and females less risk seeking, following the stressor. There was also an interaction in BOLD responses: Males in the stress condition showed greater activation in the insula and putamen while making decisions, whereas females showed the opposite pattern. Although the precise roles of these regions in this task is unclear, the insula has been implicated in signaling aversive outcomes and weighing differences in expected value in risky decision making (Clark et al. 2008), whereas the putamen is known to play a role in habitual behavior (Balleine & O'Doherty 2010).

Limited research in other decision-making domains has examined the impact of stress. Studies of intertemporal choice have found that stress exaggerates the tendency to discount future rewards in favor of smaller immediate rewards (Kimura et al. 2013) or that this effect depends on the level of perceived stress (Lempert et al. 2012). Studies of moral decision making find that stress decreases the likelihood of making utilitarian judgments in personal moral decisions (i.e., inflicting harm to maximize good consequences; Youssef et al. 2012) and correlates with egocentric moral decisions (Starcke et al. 2011). Finally, stress results in more prosocial decisions (i.e., more trust and less punishment) but less generosity as well (von Dawans et al. 2012, Vinkers et al. 2013). Most of these studies hypothesize that their findings could be attributed to the impact of stress on executive control and PFC function, although direct evidence of diminished PFC involvement due to stress in these tasks is lacking.

As this emerging research on stress and decision making indicates, a range of processes are tapped in decision-making tasks, and stress has broad, and uneven, effects on brain function. In addition, there are significant individual differences in response to stress and differential effects of chronic, acute, mild, or severe stress. In spite of these caveats, the extensive literature characterizing the impact of stress on brain function can be leveraged to understand one of the means by which an affective state might influence choices. To the extent that we can identify specific neural circuits linked to specific decision variables, such as in goal-directed versus habitual actions and model-based versus model-free decisions, we can start to characterize the distinct impact of stress.

Mood

Although stress responses are often accompanied by negative feelings, mood states are characterized primarily by subjective feelings with little concordant psychophysiological or neurohormonal changes (Scherer 2005). Research on the neural basis of moods is limited by two significant constraints. First, moods are relatively lasting states, which prevents quickly switching from one mood to another—a necessary requirement to detect within-subject differential BOLD responses, which are optimal for fMRI studies. Second, given that the primary measure of a mood state is via subjective report, it is challenging to assess moods in nonhuman animals. However, substantial psychological evidence indicates that moods affect decisions and provides some hints of the neural changes that may mediate these effects.

The influence of mood on the neural systems of decision making has been explored in a social decision-making task, the ultimatum game. In this game, there are two players: a proposer who is given a sum of money to divide with a responder, who can choose whether to accept or reject the proposer's offer. If the responder rejects the offer, both players receive nothing. In theory, the responder should accept any offer because the alternative is nothing at all. However, previous research has shown that offers around 20% of the total sum are rejected approximately half the time, presumably to punish the proposer for an unfair offer (Thaler 1988).

Studies inducing mood states prior to the ultimatum game show that participants in the role of the responder were more likely to reject unfair offers when they were in a sad (Harlé & Sanfey 2007) or disgust mood (Moretti & di Pellegrino 2010). BOLD responses during the ultimatum game were examined in two groups of participants in the role of the responder. One group underwent a sad mood induction procedure prior to scanning, and the other underwent a control, neutral mood induction task (Harlé et al. 2012). As expected, the sad mood group rejected more offers. During the presentation of unfair offers, investigators noted significantly more BOLD activation in the bilateral insula, the ventral striatum, and the anterior cingulate in the sad group relative to the control group. During the presentation of fair offers, there were no group differences in the insula; in the ventral striatum, however, the control group showed greater BOLD reward activity relative to the sad group. BOLD responses in the insula mediated the relationship between self-reported sadness and the tendency to reject unfair offers. In the context of this study, the authors suggested that the insula supports the integration of a negative mood state into the decision process. The findings in the ventral striatum are interpreted as reflecting reduced reward sensitivity when sad. This network of regions is proposed to underlie the infusion of sadness into the choice (Harlé et al. 2012).

Psychological research suggests that the infusion of mood into the computation of subjective value results from the carryover of the general action tendencies elicited by mood states onto the decision process. This proposed carryover effect is known as an appraisal tendency (Lerner et al. 2004). For example, Lerner and colleagues (2004) induced a sad, disgust, or neutral mood and explored its impact on the endowment effect—the phenomenon in which the price one is

willing to accept to sell an owned item is greater than the price one would pay to buy the same item. They found that a sad mood reversed the endowment effect (i.e., higher buy prices than sell prices), whereas a disgust mood led to a reduction in both buy and sell prices. It was suggested that sadness is an indication that the current situation is unfavorable, which enhances the appraisal of the subjective value of choice options that change the situation. Disgust, however, is linked to a tendency to move away from or expel what is disgusting, which carries over to a tendency to reduce the subjective value of all items.

Numerous studies have shown that moods also influence risky choices. For example, sad moods can increase preferences toward high-risk options, whereas anxious moods bias preferences toward low-risk options (Raghunathan & Pham 1999). Consistent with this concept, fear results in less risk seeking and anger results in more risk seeking (Lerner & Keltner 2001). Finally, positive moods can exaggerate the tendency to overweigh losses relative to gains (i.e., loss aversion) in risky gambles (Isen et al. 1988), and some of these effects of mood on risky decisions may vary by gender (Fessler et al. 2004). Studies investigating the neural systems of risky decision making have highlighted the roles of the orbitofrontal cortex (OFC) in risk-prediction errors, or in updating assessments of risk (e.g., O'Neill & Schultz 2013), and the insular cortex in the representation of risk (e.g., Knutson & Bossaerts 2007). Both of these regions have also been implicated in the representation of mood states (Lane et al. 1997, Damasio et al. 2000). Although neural evidence has yet to indicate how mood states shift the neural representation of risk assessment, this overlap in the neural circuitry mediating mood and risk provides a starting point for investigations on this topic.

Incidental Affect: Summary and Other Factors

A range of incidental affective states may bias decisions. We have highlighted two such states, stress and mood, which have different effects on choices. Stress results in changes in brain function in several regions that have been implicated in different aspects of the decision process, most notably impaired function of the PFC. To date, we know relatively more concerning stress effects on the brain than we do about how to distinguish different decision variables that engage unique neural circuits. Investigations of mood and decision making, however, are limited by the sparse literature on the neural basis of moods. The best hypothesis at this point is that moods somehow shift neural processing in regions that are involved in the assessment of subjective value, such as the OFC. Our relatively poor understanding of the neural basis of moods is exacerbated by the fact that animal models are intrinsically limited for studying phenomena characterized by subjective states. However, given the extensive psychological research on this topic, and the prevalence of mood states in everyday life, unpacking the neural mechanisms of moods and decisions is critical if we ever hope to achieve a relatively nuanced and rich understanding of human decision making.

The carryover effect of incidental affect on decisions has also been linked to other factors not discussed above because they lacked either the measurement or manipulation of affect or evidence for the underlying neural mechanisms. For instance, studies of Pavlovian-to-instrumental transfer demonstrate that actions occurring in the presence of affective Pavlovian cues are modified consistent with the motivational valence of these cues (i.e., performed with more or less vigor; see Huys et al. 2011). Both the striatum and amgydala are highlighted as regions important in integrating the affective value of the Pavlovian cue with the value of the instrumental action (e.g., Corbit & Balleine 2005, Corbit et al. 2007). A similar line of psychological research, known as affective priming, examines how the presence of an emotional cue, such as an angry or happy face, shifts subsequent choices (Winkielman et al. 2005). These studies suggest that the emotional reaction to the cue carries over to the decision. Although emotional reactions are event driven and discrete and moods are lasting subjective states that do not require an eliciting event, the

mechanism by which Pavlovian-to-instrumental transfer and affective priming are proposed to alter choices is similar to the notion of appraisal tendency discussed earlier. That is, emotional reactions, like moods, produce action tendencies that bleed over to the appraisal of the subjective value of concurrent choice options.

Finally, an understanding of the influence of incidental affect on choice behavior would be incomplete without considering how individual variability in baseline affective tendencies may alter decisions. Individuals' affect dispositions vary (Scherer 2005). For instance, some people are generally more anxious and others are more cheery. These traits with an affective flavor can influence choices, much like transient mood states. Just as anxious or fear mood states result in less risk taking, higher trait anxiety is also linked to less risky decisions, perhaps because anxiety results in more negative appraisals of subjective value (see Hartley & Phelps 2012 for a review). Of course, more extreme negative affect dispositions, such as trait anxiety, are linked to psychopathologies that have profound functional consequences, including maladaptive decisions. Accordingly, patients with anxiety disorders are more risk averse than are healthy individuals (Giorgetta et al. 2012) and are also more likely to punish in social decision-making tasks (Grecucci et al. 2013a). Given the clear link between maladaptive decisions and psychopathology, Sharp et al. (2012) proposed that decision science is an important tool to aid in our characterization of a range of psychological disorders.

EMOTION AS VALUE: HOW EMOTIONAL REACTIONS TO THE CHOICE MODULATE DECISIONS

Theories concerning the function of emotions universally highlight the role of emotions in driving actions (e.g., Frijda 2007). A classic example is the fight-or-flight response first characterized by Cannon (1915), in which a potentially threatening event (such as a predator) alters the physiological state to facilitate adaptive action (i.e., quickly escaping). Unlike the influence of incidental stress in biasing concurrent but unrelated choices, described above, in the predator example it is the choice options that evoke the emotional reaction, which in turn drives the choice. In this case, the emotional reaction is an important component of the value computation. Although this example may seem extreme, since we rarely encounter threats to our survival in our everyday lives, the principle applies in more subtle ways in our daily choices. That is, our emotional reactions to choice options or outcomes contribute to the determination of subjective value.

Emotional reactions vary widely in both intensity and quality. The neural circuits mediating the influence of emotion on choices may vary with these emotional qualities, and our understanding of the neural representation of different kinds of emotional reactions is still relatively limited. However, for emotions related to threat, extensive, cross-species research into the underlying neural circuits has been carried out. This literature provides a starting point to explore emotion's modulation of choice (see Phelps & LeDoux 2005 for a review).

The amygdala is a central component of this circuitry and is known to have a critical role in associating aversive, threatening events with neutral cues (i.e., Pavlovian fear conditioning). One of the amygdala's subregions, the lateral nucleus, is the site of synaptic plasticity linking neutral cues and aversive events. The lateral nucleus projects to both the central and basal nuclei. The central nucleus sends signals to the hypothalamus and brain stem nuclei, which mediate the physiological threat response, whereas the basal nucleus projects to the striatum. The striatum helps integrate motivation with action values, and in the presence of a conditioned threat cue, the basal nucleus input is critical for avoidance actions (LeDoux & Gorman 2001). This circuitry, with independent pathways mediating physiological threat reactions and avoidance actions, may also play a broader role in different decision contexts.

In addition to the amygdala's influence on the striatum, the amygdala has reciprocal connections with the OFC, and lesion studies in nonhuman primates have demonstrated that this connectivity with the amygdala contributes to the representation of value in the OFC (Rudebeck et al. 2013). Finally, the amygdala, the OFC, and the striatum share connectivity with the insula, a region also commonly linked to emotion's influence on decisions (e.g., Naqvi et al. 2007).

To determine how and when emotion influences the value computation, it is necessary to both measure and/or manipulate the emotional response and specify the decision variables. How emotion may influence a choice depends not only on the qualities of the emotional reaction, but also on the characteristics of the choice. Below we review studies exploring the neural systems mediating emotion's modulation of subjective value for different types of decision tasks (see **Figure 2*b*,*c***).

Risky Decisions

Risky decisions involve comparing choice options with varying probabilities of losses or gains. One of the first studies that assessed a specific emotion variable in humans and linked it to brain function used a risky decision-making paradigm known as the Iowa gambling task (IGT). The IGT presents participants with four decks of cards: two yielding small gains and losses (safe decks) and two yielding larger gains, but also occasional large losses (risky decks). Participants are asked to select cards sequentially from the different decks to win or lose money. Preferentially choosing from the safe decks results in a more favorable long-term outcome, and healthy control participants learn this through trial and error. In contrast, patients with OFC or amygdala lesions fail to shift their preference to the safe decks over time. Bechara and colleagues (1997, 1999) measured the skin conductance response (SCR), an indication of autonomic nervous system arousal, during choices and found that control participants developed an anticipatory SCR prior to selecting from the risky decks, whereas OFC- and amygdala-lesioned patients did not. The authors proposed that the anticipatory arousal response is a bodily (somatic) signal that steers participants away from less profitable, risky choices, an idea they refer to as the somatic marker hypothesis. Several studies over the years have challenged the primary assumption of the somatic marker hypothesis (Maia & McClelland 2004, Fellows & Farah 2005), a challenge further supported by evidence suggesting that autonomic responses and avoidance actions are driven by separate neural circuits (LeDoux & Gorman 2001). In spite of these caveats, this study was the first to clearly identify some of the neural circuitry mediating the integration of emotion in risky decisions.

Risky decision-making tasks vary widely, and several decision factors that influence choices may come into play. Two decision variables that are often confounded are risk sensitivity and loss aversion. Loss aversion is the tendency to weigh losses more than gains when considering the choice options. Someone who is highly loss averse may also appear to be risk averse, even if she or he is generally risk seeking in choices with minimal potential loss. Using a gambling task that enabled independent assessment of risk sensitivity and loss aversion, Sokol-Hessner and colleagues (2009) found that higher relative SCRs to losses versus gains were linked to greater loss aversion. No relationship was noted between arousal and risk sensitivity. Similarly, greater BOLD signal in the amygdala to losses relative to gains also correlated with loss aversion, but this response was unrelated to risk sensitivity (Sokol-Hessner et al. 2012). Consistent with these imaging results, patients with amygdala lesions show reduced loss aversion overall (DeMartino et al. 2010), and administering a beta-adrenergic blocker (propranolol), which has previously been shown to diminish the amygdala's modulation of memory (Phelps 2006), also reduces loss aversion but does not affect risk sensitivity (Sokol-Hessner et al. 2013). This series of studies provides strong evidence that the amygdala plays a critical role in mediating aversion to losses but that it is not linked to risk tendencies. Given that most risky decision tasks do not independently model loss

aversion and risk sensitivity, some observed effects of emotion in risky decision-making tasks may be due to loss aversion and not to risk attitudes per se.

Both the IGT and the task used by Sokol-Hessner and colleagues (2009) engage neural and physiological systems that serve to identify potential negative outcomes, prompting avoidance actions. However, other risky decision tasks have relatively few losses, as illustrated in pay-to-play games similar to slot machines, in which the only loss that occurs is when participants pay to play and do not win. Studies with these tasks have shown that emotional responses, including pleasantness ratings, SCR, and cardiovascular measures, to wins and near misses predict gambling propensity, including probable pathological gambling (Lole et al. 2011, Clark et al. 2012). These findings have been linked to increased BOLD activity in the striatum and insula during near misses (Clark et al. 2008, Chase & Clark 2010). In this decision-making context, emotions may drive people to take risky choices and not avoid them.

Another potentially important factor in risky decision-making tasks is whether the risks are known and static or unknown and changing. In dynamic and uncertain environments, the decision maker must learn the risk involved in different choices, and this risk may change over time. In dynamic, risky decision-making tasks, autonomic arousal, assessed via pupil dilation, was associated with more uncertain, exploratory decisions (Jepma & Niewenhuis 2011) and surprising outcomes (Preuschoff et al. 2011). Arousal, as well as amygdala BOLD responses, has been linked to associability (Li et al. 2011), a learning signal related to the unexpected or surprising nature of the cue, which serves to gate updating values from prediction errors coded in the striatum (see also Roesch et al. 2012). These studies suggest that in dynamic choice contexts the emotional response may be a component of ongoing predictions and evaluation necessary for learning.

Risky decision-making tasks vary widely on several dimensions, including the content of the choice (e.g., gains versus losses) and its context (e.g., static or dynamic). As the above studies demonstrate, such factors matter in part because they may shift the modulatory role of emotion: from avoiding bad outcomes to seeking favorable ones, to weighing and incorporating new information in changing environments. Future research will need to dissociate these possible roles and influences of emotion by carefully identifying the decision variables at play, the shared and separate neural circuitry used, and the underlying computations driving choices.

Social Decisions

In our everyday lives, the stimuli most likely to elicit emotional responses are other people. Social decision-making tasks investigate how choices are influenced by social context. For most of these tasks, the shift in decisions is simply due to the presence of another person, even if that person is anonymous. This observation is apparent in the ultimatum game described above in which responder participants routinely reject potential profit to punish the proposer for unfair offers. Not surprisingly, such rejections of financial gain are not observed if the proposer is a computer (van't Wout et al. 2006).

Studies examining the neural basis of rejection in the ultimatum game report an increased BOLD signal in the insula during unfair offers that is correlated with rejection rate (Sanfey et al. 2003). Arousal, assessed via SCR, was also increased during unfair offers and correlated with rejection rates—a pattern not observed when playing against a computer (van't Wout et al. 2006). In this case, the subjective value of the unfair offers was modulated by the social context of the choice. Increased physiological arousal has also been correlated with choice behavior in a social, moral decision-making task, and patients with damage to the ventromedial PFC (VMPFC), including the OFC, show both reduced physiological arousal and diminished impact of the social context on decisions (Moretto et al. 2010). The insula and OFC are two regions linked to emotion's

influence on risky decisions (see above), but in these tasks the emotional reaction is driven by the interpersonal nature of the decision, as opposed to other decision variables.

Although the simple presence of another person can evoke an emotional reaction that may influence choices, who that person is may also matter. The influence of individual characteristics in social decision making has been investigated in cross-race interactions. The impact of race group on decisions was examined using the trust game in which a participant must decide whether to invest money with a partner. Trust decisions correlated with nonconscious, negative evaluative race attitudes for Black versus White, such that participants with stronger negative implicit attitudes invested less with Black compared with White partners (Stanley et al. 2011). BOLD responses during this task showed greater amygdala activation for Black versus White partners, scaled for the size of the investment, whereas striatum activation reflected the race-based discrepancy in trust decisions (Stanley et al. 2012). These findings are consistent with a model in which the amygdala codes race-related evaluative information and the striatum integrates this information with the action value.

The impact of social factors on decisions has been demonstrated with many different decision tasks, and there have been numerous investigations of the neural circuitry and neurochemistry mediating these effects (see Rilling & Sanfey 2011, Kubota et al. 2012 for reviews). However, relatively few studies have examined whether the impact of social context on choice is related to emotional responses. Given the emotional salience of other people, it is possible that emotion mediates the influence of many social factors on decisions. Only by assessing emotional reactions during these decision tasks can we start to delineate the impact of emotion evoked by the social situation from other factors that are uniquely social.

Intertemporal Choice

Intertemporal choice tasks measure preferences between options available at different points in time. In general, people tend to prefer immediate rewards to rewards received after a delay, even when the delayed reward is larger. This phenomenon, known as temporal discounting, has been linked to many maladaptive behaviors, including poor retirement savings, obesity, and drug addiction.

Investigations of the neural systems mediating intertemporal choice have reported conflicting results. One study reported greater BOLD responses in the OFC and the striatum during choices with an immediate reward option and greater BOLD signal in the DLPFC related to choosing the delay option (McClure et al. 2004). This BOLD pattern was interpreted as supporting a theory proposed in economics (Laibson 1997) suggesting that immediate rewards engender a greater emotional response, as reflected in the striatum and OFC BOLD responses, whereas choosing the delayed reward requires cognitive control of this emotional impulse, thus engaging the DLPFC. Consistent with this proposed inhibitory role for the DLPFC, Figner and colleagues (2010) found that disrupting DLPFC function through transcranial magnetic stimulation resulted in greater temporal discounting; however, in contrast to this proposed model, so did lesions of the OFC (Sellitto et al. 2010). Another study found that BOLD signal in the VMPFC and striatum correlated with subjective value of both immediate and delayed rewards (Kable & Glimcher 2010), consistent with the known roles for these regions in the representation and updating of value (see Bartra et al. 2013 for review). The investigators suggested that increased BOLD responses to immediate reward options observed in the earlier study were due to the fact that immediate rewards generally had a greater subjective value than did delayed rewards. However, none of these studies assessed emotional responses.

To determine if emotion plays a role in temporal discounting, Lempert and colleagues (2013) measured arousal, as assessed with pupil dilation, during an intertemporal choice task. Surprisingly, emotional arousal did not reliably correlate with the subjective value of either immediate or delayed rewards, but rather this relationship varied depending on the structure of the choice set. Greater arousal responses were observed when rewards were better than expected, regardless of whether those rewards were immediate or delayed. These findings conflict with the model proposed by McClure and colleagues (2004), which suggests that it is the emotional response to the immediate choice that drives discounting, and more closely align with the study by Kable & Glimcher (2007), which proposed a unified neural representation of subjective value of immediate and delayed rewards; both may be influenced by emotion depending on the task environment.

Further support for the notion that both immediate and delayed rewards elicit emotional responses that influence choices comes from studies investigating how altering the emotional salience of the delayed reward increases patience. For example, manipulating the mental representation of a future reward to make it more concrete can change its emotional intensity and the choice. Benoit and colleagues (2011) gave participants a typical intertemporal choice task but asked them to imagine specific ways they could spend the delayed reward in the future. This manipulation increased subjective ratings of vividness and emotional intensity of the future reward and resulted in less temporal discounting. This effect was associated with increased coupling between the VMPFC and the hippocampus. A study using a similar task replicated these behavioral results and found, consistent with Kable & Glimcher (2007), that subjective value for delayed rewards correlated with BOLD signal in the striatum and the OFC, whereas activation of the dorsal anterior cingulate, and its connectivity with the hippocampus and the amygdala, mediated the change in discount rate (Peters & Buchel 2010). These same neural circuits are known to be involved in the future projection of personal events and their modulation by emotion (Sharot et al. 2007).

Studies of intertemporal choice provide a compelling example of the influence of affective neuroscience on decision science: The predominant theory used to explain the tendency to discount future rewards in economics relies on dual systems, one impulsive (emotion) and one that controls these impulses (cognitive control; Laibson 1997). As the discussion above indicates, to the extent that emotion plays a role in this behavior, emotion's contribution varies depending on the choice environment and the task structure. This variability in the role of emotion provides an opportunity for investigators to manipulate task parameters that alter emotion to influence the tendency of subjects to discount future rewards, a topic we discuss in more detail in the next section.

Emotion as Value: Summary and Related Phenomena

In addition to the decision tasks described above, emotion is also thought to contribute to subjective value computation in drug addiction, although the measurement and quantification of emotion and the understanding of the underlying neural mechanisms lag behind theory. For example, intense cue-driven motivation, termed craving, is central to addiction theory (Skinner & Aubin 2010). Cravings are a major factor that contribute to relapse, but their source is complex; studies have variously connected them to the insula (Naqvi et al. 2007), the striatum (Kober et al. 2010), and the PFC (Rose et al. 2011). Nevertheless, understanding the systems that induce these motivational desires will ultimately lead to significant advances in the treatment of such disorders of choice.

A primary function of emotion is to provide a signal to the organism that a stimulus or event may be relevant for present or future survival or well-being (e.g., Frijda 2007). Thus it is not surprising that emotional reactions modulate a range of cognitive functions, such as memory, attention, and

perception (Phelps 2006). It is also not surprising that part of the calculation of the value of decision options should include the nature of the emotional response elicited by those options or potential outcomes. How this occurs, however, varies depending on the decision variables assessed and the specific emotional reaction. As our review of this literature indicates, there is likely a collection of neural circuits underlying emotion's modulation of the value calculation.

Across studies of the neural basis of decision making, the OFC/VMPFC and the striatum are cited as necessary for the coding of subjective value; the striatum is specifically linked to updating values from reinforcement (prediction errors) via dopaminergic projections from the ventral tegmental area (e.g., Bartra et al. 2013). The studies outlined above examining the impact of emotion also implicate, in addition to these regions, the insula and amygdala. The insula is a large region linked to numerous functions relevant to decision making, including the anticipation of pain (Ploghaus et al. 1999) and monetary loss (Knutson & Bossaerts 2007), as well as the representation of disgust (Phillips et al. 1997) and physiological arousal (Critchley et al. 2000). A recent meta-analysis of fMRI studies examining the coding of subjective value found, not surprisingly, that the OFC/VMPFC and the ventral striatum emerged as two regions with BOLD responses that positively correlate with subjective value. In contrast, the insula, along with some other striatal regions and the dorsomedial PFC, showed greater BOLD responses for both more positive or negative subjective value. Bartra et al. (2013) suggest that the insula may integrate emotional salience or arousal linked to the decision variables into the value computation, regardless of its valence. As mentioned above, connectivity between the amygdala and the ventral striatum is critical for enabling avoidance behavior to acquired threats (LeDoux & Gorman 2001), and the amygdala contributes to value coding in the OFC (Rudebeck et al. 2013). The amygdala may play a role in avoidance across a range of decision tasks (e.g., Stanley et al. 2012, Sokol-Hessner et al. 2013), as well as in modulating learning from both positive and negative reinforcement more broadly (e.g., Roesch et al. 2012; Murray & Rudebeck 2013) (see **Figure 2*b*,*c***). The limited research to date on the integration of emotion into value computation is starting to yield a network of regions, but our understanding of precisely how these regions interact in more complex human decision-making tasks is still relatively unclear.

CHANGING AFFECT, CHANGING CHOICES

Clinical interventions for a range of psychopathologies are focused on changing affect. Outside the clinic, the ability to regulate the appropriateness of emotional responses to circumstances is a major component of healthy, adaptive social behavior and well-being. Although we often describe emotions as reactions to environmental stimuli that are beyond our control, affective scientists have long recognized the fluidity of our emotional lives and our ability to alter or determine our emotions. A major focus of basic research in affective neuroscience over the past decade has been to understand how emotions can be modified and how we can utilize this flexibility of emotion to develop more effective clinical interventions or more satisfying and healthy lives (Hartley & Phelps 2010, Davidson & Begley 2012).

To the extent that affect and emotions are incorporated into the assessment of subjective value, changing emotions should also change choices. Although several techniques have been used to change emotion in the laboratory across species (see Hartley & Phelps 2010 for a review), and all these techniques are presumed to influence later choices, only a few have been implemented directly during decision-making tasks to assess how choices are altered. Below we review the research examining one such technique and highlight some other potential mechanisms for future investigation (see **Figure 2*d***).

Cognitive Emotion Regulation

The common wisdom that one can see the glass as half full or half empty captures the essence of cognitive emotion regulation. Our emotional reactions are determined, in part, by how we appraise or interpret the circumstance or event (Scherer 2005). Although some individuals may have a general tendency to see the world in a positive or negative light, the ability to shift emotion through changing one's interpretation of an event, known as reappraisal, can also be taught and consciously applied. In a typical reappraisal task, the participant is asked to think about the stimulus differently to reduce its negative emotional consequences.

Many studies have investigated the neural systems that mediate the cognitive regulation of negative emotions as assessed through subjective reports or physiological responses (see Ochsner & Gross 2005). They typically report increased DLPFC BOLD responses during regulation versus attend conditions accompanied by decreased amygdala activation. The DLPFC is proposed to implement the executive control needed to actively reinterpret the stimulus during reappraisal, whereas the amygdala is involved in the expression of the emotional response. There is relatively sparse direct connectivity between the DLPFC and amygdala, so it is unlikely that the DLPFC directly influences amygdala function but rather does so through more ventral PFC regions. The VMPFC is known to have reciprocal connections with the amygdala that inhibit emotional reactions following extinction learning in Pavlovian fear-conditioning tasks, and it is proposed to mediate the influence of the DLPFC on the amygdala (Delgado et al. 2008b); however, other studies have suggested that the ventrolateral PFC (VLPFC) plays this role (Buhle et al. 2014). This DLPFC-VMPFC/VLPFC-amygdala circuitry is thought to underlie the cognitive control of diminishing negative emotional reactions, but it may also play a role in increasing negative affect depending on the reappraisal strategy (Otto et al. 2014). Emotion regulation strategies can also be employed to reduce arousal associated with anticipated monetary reward. These strategies engage overlapping regions of the DLPFC and VMPFC and yield decreased BOLD reward responses in the striatum (Delgado et al. 2008a). A similar circuitry has been implicated in the cognitive control of cravings (Kober et al. 2010).

In a risky decision-making task, a reappraisal strategy altered both arousal and choices. As described earlier, Sokol-Hessner and colleagues (2009) found that the relative SCR response to losses relative to gains correlated selectively with loss aversion but was unrelated to risk sensitivity. A similar pattern was observed for amygdala BOLD signal (Sokol-Hessner et al. 2013). In a variation of this task, participants were instructed to reappraise the significance of the choice by thinking of it as one of many, or to "think like a trader" building a portfolio. Using this strategy reduced the SCR to losses, and this reduction was correlated with diminished loss aversion, with no effect on risk sensitivity (Sokol-Hessner et al. 2009). Mirroring the SCR results, reduced amygdala BOLD responses to losses during regulation also correlated with a reduction in loss aversion. In contrast, baseline BOLD responses in the DLPFC, VMPFC, and striatum increased with regulation (Sokol-Hessner et al. 2013). These findings suggest that using a reappraisal strategy to change emotion and choices engages the same neural circuitry that is observed in more typical emotion regulation tasks. A similar reappraisal strategy that either emphasized or de-emphasized the importance of each individual choice was found to both increase and decrease subjective value in a risky decision task (Braunstein et al. 2014). In addition, in an intertemporal choice study described above, reframing the interpretation of a future reward resulted in more patience (Benoit et al. 2011).

Emotion regulation strategies have also been used to change the tendency to punish in the ultimatum game. Van't Wout and colleagues (2010) asked participants to play the ultimatum game while utilizing a cognitive emotion reappraisal strategy. In the responder role, participants

who reappraised the motivations of the proposer in suggesting an unfair offer were less likely to reject it. This cognitive emotion regulation manipulation carried over to future choices. When the participants were subsequently put in the proposer role, they were less likely to propose unfair offers. In a follow-up fMRI study, participants in the responder role were asked to imagine either negative intentions of the proposer or positive intentions. Relative to a baseline condition, these reappraisal strategies resulted in rejecting more or fewer unfair offers, respectively, and subjective emotional responses varied as well. Consistent with previous research, activation of the insula predicted the rejection of unfair offers (Sanfey et al. 2003, Harlé et al. 2012), and the regulation strategies resulted in both increased insula BOLD responses with the negative intention strategy and decreased BOLD signal with the positive intention strategy. As expected, given the general emotion regulation circuitry outlined above, the DLPFC showed increased activation during both reappraisal conditions relative to baseline (Grecucci et al. 2013b).

As these studies indicate, cognitive emotion regulation techniques are flexible strategies that can rapidly change emotional reactions. The reappraisal strategies described above were adapted to the specific decision situation but had the same effect of altering the emotional response and modulating decisions, and they engaged typical cognitive emotion regulation regions. This confluence of evidence provides strong support for the notion that emotion is a critical component of the assessment of subjective value in these tasks because changing emotion also changed the choice.

Changing Affect: Summary and Other Potential Techniques

The notion that changing affect alters decisions was also demonstrated in the incidental affect manipulations described above. In those studies, inducing stress or a mood in the laboratory changed choices. In contrast, cognitive emotion regulation techniques alter choices by changing the appraisal of the decision variables that elicit emotional reactions. These techniques are powerful because they are flexible, can alter emotion in different ways, and can be quickly acquired and utilized without changing the situation. However, they require an effortful application of the strategy, which may not always be ideal. With practice, these strategies may become more automatic and less deliberate. Consistent with this, novice stock traders have demonstrated more physiological arousal to volatility in the stock market, a finding attributed to loss aversion, as compared with more senior stock traders, who show less arousal and better choices (Lo & Repin 2002), perhaps resulting from a broader perspective on market volatility gained from experience.

Although the flexibility of cognitive emotion regulation techniques can be an advantage, there are also some potential disadvantages. Cognitive emotion regulation strategies are less successful in stressful situations (Raio et al. 2013), perhaps owing to their dependence on the DLPFC. In addition, when emotional reactions consistently result in maladaptive choices, it may be useful to have a technique that leads to a more lasting change. Affective neuroscience has identified a few such strategies, but their impact on emotional reactions linked to decision making has not yet been widely investigated. For example, extinction training has been used to reduce acquired affective responses by repeatedly presenting the cue without the associated reinforcement. Although this technique can be effective, it leaves the original association intact; thus the unwanted affective response may return. To induce a more lasting change in learned associations underlying emotional responses and instrumental actions, researchers have recently investigated techniques that change the original associative, affective memory by altering its re-storage after retrieval or reconsolidation. Our understanding of reconsolidation mechanisms and how to target these processes in humans is still in its infancy, but this technique may lead to exciting advances in reducing the impact of maladaptive emotional reactions on choices (see Hartley & Phelps 2010 for a review).

Finally, an interesting twist in investigations examining the relation between emotion and decision making is that choices themselves can alter emotions. For example, animals given the opportunity to learn to avoid shocks show a lasting benefit, exhibiting diminished fear responses and faster and more robust extinction in subsequent tasks in which they do not have control over the shock reinforcer (Maier & Watkins 2010, Hartley et al. 2014). This research suggests that this persistent impact of choice on future threat reactions results from alterations in the brain stem–prefrontal–amygdala circuitry underlying the generation and control of learned threat associations (Maier & Watkins 2010). In humans, the opportunity for choice enhances subjective affective ratings of choice options and concurrently increases BOLD reward responses in the striatum (Leotti & Delgado 2011, 2014). Psychological theories have emphasized the importance of perception of control over one's environment on well-being (e.g., Bandura et al. 2003), as well as the impact of choices on preferences (e.g., Festinger 1957). Studies examining the neural basis of the impact of choice on emotional reactions and preferences (e.g., Sharot et al. 2009) are starting to provide a neurobiological framework for these psychological findings.

To the extent that affect and emotion influence choices, changing affective responses will alter our decisions. The emerging research on techniques to change affect shows that a range of mechanisms to modify emotions can be differentially applied in different decision contexts. Some are flexible and rapid, such as cognitive emotion regulation, and others are more lasting, such as targeting reconsolidation. In addition, choices themselves can change affect, which in theory should change subsequent choices. If we can discover and characterize more effective means to alter emotion, we should be able to harness these techniques to help optimize decisions.

MOVING PAST DUAL SYSTEMS TO MULTIPLE MODULATORY NEURAL CIRCUITS

In this overview of the current neuroscience literature exploring the relationship between affect and decision making, we have attempted to identify the neural circuits that mediate this interaction. What is emerging is clearly incompatible with the notion of two systems. Rather the literature suggests that there are multiple neural circuits underlying the modulation of decision making by emotion or affect. As our breakdown of affective components and decision tasks demonstrates, the specific neural circuits involved vary depending on which affective component is engaged and which decision variables are assessed. Thus, we suggest an alternative approach to understand the relation between emotion and decision making, which entails characterizing and identifying the multiple neural circuits underlying the different means by which emotion and affect influence decisions (see also Sanfey & Chang 2008).

Of course, this multiple modulatory neural circuits approach is not nearly as parsimonious as the dual systems account, and one could argue that dual systems is simply a rough and useful heuristic to characterize the role of emotion in decision making. Although referring to the heart and head may be useful in thinking about some types of decisions outside the laboratory, the reference to dual systems as the primary psychological and neural theory for understanding the relationship between emotion and decisions is still relatively common in the scientific literature (e.g., Cohen 2005, Greene 2007, Figner et al. 2009, Reyna & Brainerd 2011, Paxton et al. 2012). Much as some researchers have suggested that scientists abandon the limbic system concept because its continued use impedes progress in understanding the detailed and complex neural basis of affect (LeDoux 2000), we argue that the repeated reference to dual systems of emotion and reason in research on decision making potentially limits scientific advances by discouraging investigations that capture the detailed and nuanced relationships between unique aspects of affect and choices. Furthermore, it suggests to the layperson and scientists in other disciplines that the intuitive and historical notion

of competing forces of emotion and reason is based on scientific fact. Perpetuation of this idea may dampen enthusiasm for efforts to further explore the complex interactions of affect and decision making and may result in the development of potentially misguided or nonoptimal techniques to inhibit emotion in order to promote rational decision making.

Despite its complexity, our proposed conceptualization of the relationship between affect and decision making begins to capture the subtleties involved in understanding their interaction. Both affect and decision making are general terms that describe a collection of factors and processes, only some of which are explored above. Investigating affect and emotion is challenging by itself, both because manipulating and measuring affect in the laboratory is difficult and because there is debate about how best to characterize affective variables. Differentiating the collection of unique variables that influence choice in any given situation is also challenging for decision science. In spite of these caveats, initial attempts to measure or manipulate affective components and to relate them to specific aspects of decision tasks have yielded exciting advances. As the disciplines of affective neuroscience and neuroeconomics advance, we can build on this progress to further characterize the multiple neural circuits that mediate the modulatory relationship between emotion and decision making.

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