

Emotion, Decision Making, and the Amygdala

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Emotion plays a critical role in many contemporary accounts of decision making, but exactly what underlies its influence and how this is mediated in the brain remain far from clear. Here, we review behavioral studies that suggest that Pavlovian processes can exert an important influence over choice and may account for many effects that have traditionally been attributed to emotion. We illustrate how recent experiments cast light on the underlying structure of Pavlovian control and argue that generally this influence makes good computational sense. Corresponding neuroscientific data from both animals and humans implicate a central role for the amygdala through interactions with other brain areas. This yields a neurobiological account of emotion in which it may operate, often covertly, to optimize rather than corrupt economic choice.

Introduction

The disregard that human choice frequently pays to the axioms of formal decision theory has placed a high premium on developing a biological understanding of the structure that underlies it. Researchers from behavioral economics, finance, marketing, and politics are now looking to neuroscience to provide insights into the peculiarities of choice that often plague their own domains. Reliance on a traditional two-system model, in which a “cold,” rational, far-sighted cognitive system battles against a “hot,” irrational, short-sighted emotional system (Camerer et al., 2005; Kahneman and Frederick, 2002; Sloman, 1996), is beginning to prove inadequate in light of contemporary psychological and neurobiological data that favor multiple decision-systems (Figure 1). The latter perspective promises a more mechanistic account of decision making but leaves open the question of exactly what was captured by traditional concepts of an emotional system, this having provided such an enduring repository for the various anomalies that have proved problematic to accommodate.

The brain structure most commonly affiliated with emotion is the amygdala, predominantly due to its widely studied role in Pavlovian (classical) conditioning. Indeed, the acquisition of innate value and responding in Pavlovian paradigms plays a central role in most standard neurobiological accounts of emotion (Dolan, 2002; LeDoux, 2000a; Rolls, 1998). However, recent animal and human studies suggest that the amygdala may also play an important role in guiding choice. Understanding how these two aspects of amygdala function can be integrated focuses attention on experimental studies that suggest that the information acquired in Pavlovian learning might guide more sophisticated action-selection processes underlying decisions. Here, we review evidence, which draws strongly on studies of Pavlovian-instrumental interactions, that addresses this more elaborate role for the amygdala. The resulting decision phenotype is typically emotional but arises from underlying processes that are generally rational and whose effects might often only become *apparent* in instances when they cause deviations from rationality.

We begin by reviewing the nature of Pavlovian conditioning, in which we consider both the innate responses it evokes and the

type of information it learns, which embodies the notion of Pavlovian (both appetitive and aversive) value. We then show how several key experimental paradigms illustrate how other (instrumental) action systems can exploit this information to refine their own performance. By addressing theoretical considerations, we illustrate that these processes may often maximize the use of information acquired through different learning mechanisms to optimize choice. We then review the experimental evidence in animals that implicates the amygdala in the control of many of these aspects of decision making. Finally, concentrating on decision making in humans, we draw parallels with results from behavioral economics that might be understood in terms of these underlying, amygdala-dependent processes.

Pavlovian Learning

Pavlovian learning provides a unique means to learn the motivational landscape of the environment, by coupling experience-based statistical learning with the wisdom of species-wide evolutionary inheritance. In the classic experimental paradigm, a neutral cue, such as switching on a light, reliably precedes an important event, such as the arrival of food. Learning the predictive relationship between the two events has two key consequences. First, it allows an appropriate response to be evoked in anticipation of the outcome, such as approach and salivation. Second, it endows the otherwise uninteresting cue with acquired motivational value, reflecting the utility of the net reward or punishment that it predicts. As we shall discuss, this value turns out to be a very useful quantity that can be adaptively exploited by other decision-making systems, particularly when faced with potentially complex choices.

Pavlovian Responses

Konorski (1967) first formalized the types of action evoked when animals are faced with a motivationally salient event (unconditioned stimulus) or a cue predictive of a salient event (conditioned stimulus). He classified actions into those specific to the identity of the outcome, termed “consummatory responses,” such as salivating when faced with foods, and those more generally appropriate to the valence of the outcome, such as approach and withdrawal, termed “preparatory responses.”

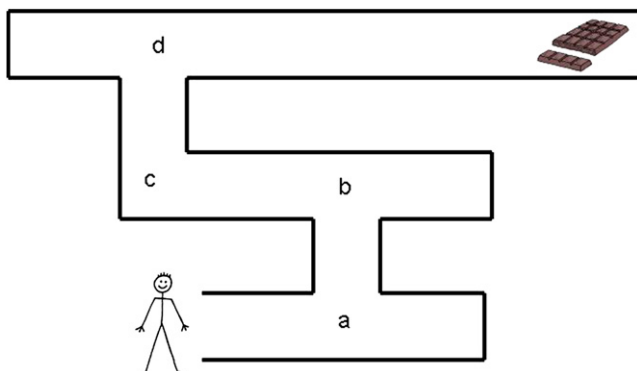


Figure 1. How Many Action Systems?

Consider the problem of learning to find the food in the maze above. First, the simplest solution utilizes Pavlovian conditioning and exploits innate actions such as approach and withdrawal. During Pavlovian conditioning, positions that are associated with the outcome acquire a positive value that causes the agent to approach them. Thus, following the tendency to approach the reward from position **d**, **d** will acquire a positive utility, causing it to be approached from other positions, including **c**. Through sequential conditioning, the individual can potentially navigate relying purely on the Pavlovian approach.

Second, habits involve the learning of action utilities. Trial and error will reveal that turning right at **d** is immediately profitable, and the reward can be used directly to reinforce the action. Learning the preceding actions, such as what to do at position **b**, is more difficult, because the outcomes are both delayed and contingent on subsequent actions (the credit assignment problem; Bellman, 1957). One possibility is to use either the subsequently available best action utility (as in Q learning; Watkins and Dayan, 1992) or the subsequent Pavlovian state values (as in Actor-Critic learning; Barto, 1995) as a surrogate reward indicator. This has the effect of propagating (or “bootstrapping”) action utilities to increasing distances in chains of actions.

Third, goal-directed learning mechanisms overcome the lack of an explicit representation of the structure of the environment or of the utility of a goal in Pavlovian actions and habits by involving a model of some sort. Indeed, there may be more than one distinct form of model-based decision system (Yoshida and Ishii, 2006). A natural form is a map of the area within which one’s own position and the position of the goal can be specified, in which the structure of the model is governed by the two-dimensional physical nature of the environment. Alternatively, propositional models, which have a less-constrained prior structure, might specify actions as bringing about transitions between uniquely identified positional states. Such models bear a closer relation to linguistic mechanisms, for instance taking the form of “from the starting position, go left, left again, then right, and then right again,” and in theory have the capacity to incorporate complex sets of state-action rules.

Fourth, and finally, control might also be guided by discrete episodic memories of previous reinforcement. Such a controller is based on explicit recall of previous episodes and has been suggested to guide actions in the very earliest of trials (Lengyel and Dayan, 2007).

Pavlovian responses are by and large appropriate, insofar as it makes sense to approach food and salivate in anticipation of eating it, and it makes sense to withdraw when seeing a predator. Pavlovian conditioning allows these apparently hardwired responses to be elicited as soon as a prediction is reliably made. In this way, Pavlovian responses reflect a base set of evolutionarily inherited hardwired actions, remarkably, though not exclusively (Bolles, 1970), conserved across species.

Accordingly, situations in which Pavlovian actions are inappropriate often reflect either a change in environment that is out of pace with evolution or the mischievous paradigms of experimental psychologists. The former is best illustrated by over-eating in humans. The abundance of food in many modern societies renders the beneficial effect of a feeding system that

evolved in much sparser environments inappropriate in light of known health sequelae of excessive eating. However, a goal-directed action system that can exploit this explicit knowledge struggles to compete with its Pavlovian counterpart and in Western societies may have contributed to an epidemic of obesity. Indeed, the only “cure” for such Pavlovian gluttony may itself be Pavlovian, insofar as contingently pairing nausea and vomiting with food results in a food aversion capable of inhibiting Pavlovian compulsion but, unfortunately, only if food is relatively novel (Best and Gemberling, 1977).

More spectacular examples of Pavlovian “impulsivity” exist in the experimental domain (Dayan et al., 2006). In his famous experiment, Hershberger (1986) placed chicks in front of a food cart and arranged the cart to move in the same direction as the chick, but at twice the speed. Consequently, approaching the cart caused it to retreat at twice the speed, but retreating from the cart causes it to approach the chick. Chicks’ inability to learn to move away from the cart can be explained by the dominance of a preparatory Pavlovian impulse to approach it over an instrumental ability to learn to retreat and obtain the food.

In a broader sense, Pavlovian actions reflect the sorts of actions that evolution prescribes as almost invariably appropriate. Indeed, in the aversive domain in particular, responses such as in freeze and flight in situations of threat may clearly be life saving. In isolation, such responses reflect decisions in their own right. In terms of optimal control, they can be thought of as a set of action priors, over and above which instrumental systems may operate. In the situations in which such decisions are inappropriate, the resulting competition between other action systems is manifest as instances of impulsivity or failed self control.

Pavlovian Values

Beyond basic responses, Pavlovian learning provides a mechanism by which the predictive value of a cue or state can be learned. This “value” reflects the sum of rewards and punishments expected to occur from a given point in the environment, yielding information that has potential uses beyond directing Pavlovian “actions.” Accordingly, experimental psychologists have developed several ingenious learning paradigms that illustrate just how Pavlovian values are exploited by other systems (Figure 2) (Dickinson and Balleine, 2002; Mackintosh, 1983).

In the paradigm termed “conditioned reinforcement,” an animal is first taught the Pavlovian contingency between a cue and a reward (Fantino, 1977; Hyde, 1976). Subsequently, it is then exposed to the instrumental contingency between an action, such as a lever press, and the cue. Even though the cue is presented entirely in extinction, allowing no direct instrumental learning of the reward that it previously predicted, the animal will start to press to the lever, indicating critically that the acquisition of Pavlovian value by the cue is, alone, able to reinforce instrumental action systems.

A slightly more complex illustration of Pavlovian-instrumental cooperation is seen in avoidance learning, in which it deals with the problem of how to reinforce actions that lead to apparently neutral outcomes (which represent instances of successful avoidance) (Mowrer, 1947). Specifically, Pavlovian fear mechanisms are thought to motivate escape responses when a punishment is predicted, and subsequent avoidance is driven by appetitive reinforcement of the state that marks the safety of

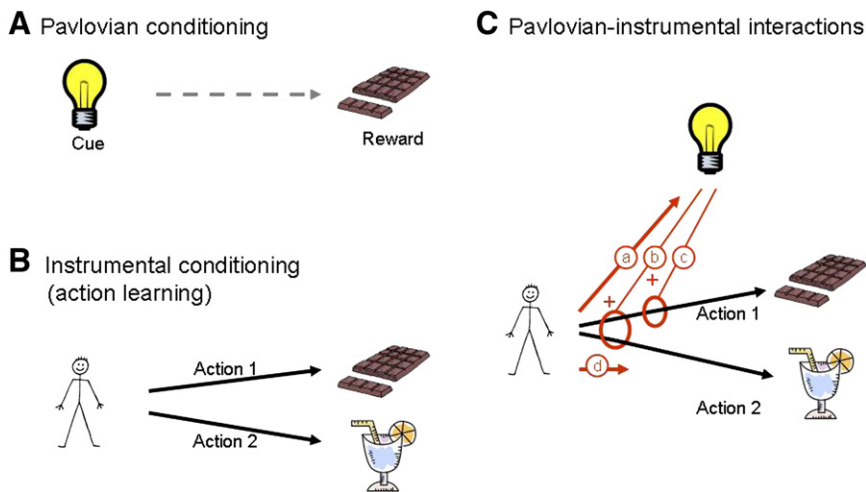


Figure 2. Pavlovian and Instrumental Learning and Their Interactions

(A) Pavlovian conditioning. Repeated sequential presentations of a cue (light) followed by a reward (chocolate) allow an individual to learn that the cue predicts the reward.

(B) Instrumental conditioning (action learning). An individual learns that action 1 (for example, pressing a button) leads to delivery of a particular reward (chocolate). This reinforces the action whenever it becomes available. A different action (for example, spinning a wheel) leads to delivery of a different reward (a refreshing drink), which reinforces action 2.

(C) Pavlovian-instrumental interactions. The Pavlovian cue (light) is sometimes presented when various actions are available. This will reinforce any action seems to lead to delivery of the cue (conditioned reinforcement) labeled (a), all other reward-predicting actions (actions 1 and 2, general Pavlovian-instrumental transfer) labeled (b), chocolate-associated actions (action 1, specific Pavlovian-instrumental transfer) labeled (c), or approach responses (Pavlovian conditioned responses) labeled (d).

successful avoidance, which has the form of a Pavlovian conditioned inhibitor (a Pavlovian cue that predicts the omission of punishment) (Bolles and Grossen, 1969; Bouton, 2006; Crawford et al., 1977; Damato et al., 1968; Dickinson, 1980; Dinsmoor, 2001; Starr and Mineka, 1977). In this case, it is the Pavlovian conditioned inhibitor that adopts the role of conditioned reinforcer.

Pavlovian values can also influence actions in a slightly subtler way. In Pavlovian-instrumental transfer, a Pavlovian cue is first trained to passively predict a particular reward. Next, the individual is trained on an instrumental learning paradigm, such as a lever-press, for either the same or different reward. Finally, the Pavlovian cue is presented at the same time as the instrumental behavior, usually in extinction. In both animals and humans, the appetitive Pavlovian cue increases the rate of instrumental appetitive responding, independently of the identity of the reward, reflecting a general increase in response vigor (general Pavlovian-instrumental transfer) (Dickinson and Balleine, 2002; Estes, 1948; Lovibond, 1983). And in a similar manner, an aversive cue will reduce responding (conditioned suppression) (Digusto et al., 1974; Estes and Skinner, 1941). However, it turns out that Pavlovian values can be integrated more selectively with choice, illustrated by specific reinforcer effects in transfer paradigms. For example, if an animal that is both hungry and thirsty is able to perform separate actions to obtain food or water, a Pavlovian cue previously associated with food will increase the number of times the animal selects the food-related action. Alternatively, if the individual is sated for one or other reward (i.e., is allowed to drink or eat freely), then the transfer effect is appropriately directed at the nonconsumed reward (Balleine, 2001).

In humans, it seems likely that many everyday emotional influences on decision making may be related to phenomena captured in the experimental paradigms developed by animal learning theorists (Phelps and LeDoux, 2005), evidenced for instance by the success of marketing and advertising campaigns that exploit passive, emotionally laden cues. More directly, overeating in the context of appetitive cues has clear parallels with conditioned potentiation (Holland and Petrovich, 2005) (see below). Addictive and compulsive behavior is thought to

be strongly related to conditioned reinforcement and Pavlovian-instrumental transfer (Everitt and Robbins, 2005). In behavioral economics, so-called “framing” effects, in which the emotional valence of the language in which options are described dramatically changes people’s risk preferences (Kahneman and Tversky, 2000; McNeil et al., 1982), resemble the effects seen in transfer paradigms (De Martino et al., 2006). Furthermore, people’s tendencies to overvalue losses in comparison to gains, apparent in loss aversion, has been suggested to be related to the dominance of automatic responses to losses (Camerer, 2005; Trepel et al., 2005). And in a further example from behavioral economics, the “hot stove” effect, which describes the bias away from collecting information (such as about the temperature of stoves) about previous events with aversive consequences, is a direct parallel to the avoidance “paradox” (Denrell and March, 2001).

Theoretical Aspects of Pavlovian Control

Insight into the importance of Pavlovian interactions can be gained by considering the type of information that Pavlovian values carry. Allowing assumptions about temporal discounting, Pavlovian cues provide an indication of the average amount of reinforcement available at a given time, which turns out to be a potentially very useful signal. First, it provides a standard against which individual actions should be judged. For example, receiving £5 is positive in a neutral context, but negative in the context of cues that suggest that an average outcome should be £10. In terms of choice, this may change the relative utilities of available options for individuals with nonlinear utility functions. But more importantly, it may change the values of actions as they are acquired through learning. Learning how much better or worse the value of a current state is before and after taking a particular action, rather than directly learning absolute action values, proves to be a much more efficient way of learning optimal actions in situations in which Pavlovian state values are known with greater relative certainty. Indeed, using state-based values to learn action values is central to several popular learning rules, notably the actor-critic and advantage learning models, which have modest biological support (Baird, 1993; Dayan and Balleine, 2002; O’Doherty et al., 2004).

Second, such relative judgments may influence further learning by controlling exploration. Exploration is critical in environments when the outcomes of actions are either not known with certainty or change over time. The strategy used for exploration has an important effect on apparent risk attitudes (Denrell, 2007; March, 1996; Niv et al., 2002). This is because if the value of an action is uncertain then the relative value of an outcome determines the frequency with which it is sampled: an option judged aversive will be tried less often than one judged positive. Thus, Pavlovian values can modify asymmetrical sampling biases that arise between positive and negative or high versus low variance outcomes.

Third, in addition to judgments of *relative* utility, Pavlovian values can also usefully inform how much effort an individual should invest in a set of actions. This notion embodies the concepts of excitement and motivational vigor and can be rationalized in any system in which there is an inherent opportunity cost to performing an action (Niv et al., 2007). If the average return is judged high by a Pavlovian system, then it makes sense to invest more effort in instrumental actions, as seen in general Pavlovian-instrumental transfer.

Fourth, and more specifically, Pavlovian values can selectively guide choices among different options presented simultaneously. Pavlovian cue value reflects a state-based homeostatic quantity that reflects physiological need. Thus, the utility of food declines as one becomes satiated, or the utility of shelter is reduced on a fine, warm day. This information can be used to judge the specific utilities in situations in which many courses of action exist, as is demonstrated by sensory-specific satiety. Indeed, one of the paradigms (devaluation) that has been particularly instructive in dissociating different action systems draws on the fact that habit-based learning systems are unable to access specific value-related information without experiencing outcomes and relearning actions (Balleine, 1992).

The Role of the Amygdala Pavlovian Learning

The amygdala is widely recognized as one of the principle brain structures, along with the striatum, associated with Pavlovian learning (Gallagher and Chiba, 1996; Klüver and Bucy, 1939; LeDoux, 2000a; Maren and Quirk, 2004; Murray, 2007). Broadly, it consists of two functionally and anatomically distinct components, namely those that are affiliated with the central and basolateral nuclei. Both are heavily connected with extensive cortical and subcortical regions, consistent with a capacity to influence diverse neural systems (Amaral and Price, 1984).

Early theories on the role of the amygdala centered on fear (Weiskrantz, 1956), in light of the discovery that it acts as a critical seat of Pavlovian aversive conditioning (Maren, 2005; Quirk et al., 1995). More specifically, many elegant experiments have demonstrated that the basolateral amygdala, by way of its extensive afferent input from sensory cortical areas, is critical for forming cue-outcome associations and that the central nucleus is critical for mediating conditioned responses, by way of its projections to mid-brain and brainstem autonomic and arousal centers (Kapp et al., 1992). In what became known as the “serial model” of amygdala function, the basolateral amygdala is thought to learn associations, with direct projections to central

amygdala engaging the latter to execute appropriate responses (LeDoux, 2000b).

In subsequent years, several key findings have emerged that have enriched this picture. First, the amygdala has been found to be critically involved in appetitive learning, in a similar (though not identical) way to its involvement in aversive learning (Baxter and Murray, 2002). Second, the central and basolateral nuclei often operate in parallel as well as in series. This is thought to subserve dissociable components of learning, whereby the central nucleus mediates more general affective, preparatory conditioning, with the basolateral nuclei mediating more consummatory, value-specific, conditioning (Balleine and Killcross, 2006; Cardinal et al., 2002). Third, rather than just executing Pavlovian responses, connections of both central and basolateral amygdala with other areas, such as the striatum and prefrontal cortex, are critical for integrating Pavlovian information with other decision-making systems (Cardinal et al., 2002).

The Acquisition of Value

Single-neuron recording studies have identified neurons that encode the *excitatory* Pavlovian value of rewards and punishments as well as neurons that encode salient predictions independently of valence (Belova et al., 2007; Paton et al., 2006). Values can also be *inhibitory*, as a consequence of the opponent relationship between appetitive and aversive systems. Such opponency comes in two forms: that related to the omission of an expected motivational stimulus (Konorski, 1967) and that related to the offset of a tonic motivational stimulus (Solomon and Corbit, 1974). Notably, the amygdala is implicated in encoding both (Belova et al., 2007; Rogan et al., 2005; Seymour et al., 2005).

Behavioral models of Pavlovian learning suggest that values are acquired in a manner that depends on the discrepancy between predicted and actual outcomes (Rescorla and Wagner, 1972), and such prediction-error-based learning rules have accumulated significant biological support in another structure strongly implicated in Pavlovian learning, namely the striatum. This is the case for both appetitive learning, thought to be guided by dopaminergic projections from the ventral tegmental area in the midbrain (Nakahara et al., 2004; Satoh et al., 2003; Schultz et al., 1997), and aversive learning, evidenced in humans by fMRI (Jensen et al., 2007; Seymour et al., 2004). In both cases, the nature of learning follows a class of updating algorithm (called temporal difference models) that bootstrap value predictions using *temporal* prediction errors and learn using both positive and negative prediction errors. This provides a flexible mechanism to learn values ideally suited to environments with delayed and uncertain outcomes.

The algorithmic nature of value learning in the amygdala is less clear. Human fMRI studies have suggested that aversive Pavlovian values are acquired in amygdala in a dynamic fashion consistent with prediction-error-based models (Glascher and Buchel, 2005; Yacubian et al., 2006), and prediction errors occurring at the time of outcome have been reported. A recent single-neuron study of probabilistic appetitive and aversive conditioning in monkeys has shown that separate neuronal populations encode valence-specific, probabilistic, value-related signals (i.e., modulated by outcome uncertainty) (Belova et al., 2007). This study also found activity in keeping with a mirrored opponent pattern, in which some neurons coded both reward and omitted

punishment and vice versa. However, no cells intrinsically displayed a full prediction error pattern, suggesting that learning might be driven by a temporal prediction error signal arising from elsewhere.

There are other reasons for thinking that the Pavlovian processes seen in amygdala are not the same as those seen in striatum, and one of the most significant reasons relates to the representation of negative prediction errors (Redish et al., 2007). In particular, aversive extinction (in which aversive outcomes are omitted) is known to be mediated by active learning that involves inputs from medial prefrontal cortex, in contrast to the more direct acquisition of excitatory values (Maren and Quirk, 2004; Milad and Quirk, 2002). Such extinction memories are easily “forgotten” or disrupted by procedures such as reinstatement and are sensitive to reconsolidation (Duarci et al., 2006). This aversively biased asymmetry endows amygdala-based Pavlovian values with the same sort of “safety-first” encoding that reflects the affective hardwiring of unconditioned stimuli. Thus, it is possible that the temporal-difference-based mechanisms of Pavlovian value learning in striatum reflect a mechanism that may be to a certain extent distinguishable and perhaps computationally more flexible than that implemented in amygdala, but with both using prediction errors.

These differences may extend to the way in which Pavlovian values influence decision making. Despite early models, it is unclear whether a striatal dopamine system exploits a learning mechanism (for example, actor-critic) that directly utilizes Pavlovian predictions (or their errors) for action learning (Daw, 2007; Morris et al., 2006; Roesch et al., 2007; Samejima et al., 2005), which would be necessary for Pavlovian effects on choices, as seen in conditioned reinforcement, to have direct access to actions values. Accordingly, this focuses attention elsewhere to determine the components of a coordinated system that mediates Pavlovian-instrumental interactions and on experimental studies that attempt to disrupt them.

Pavlovian-Instrumental Interactions in Animals

There is good evidence that the amygdala yields Pavlovian values to instrumental action systems, and indeed, central and basolateral amygdala appear to mediate distinct types of interaction. For instance, Killcross et al. (1997) took rats with either central or basolateral lesions, first trained them in a Pavlovian conditioning procedure, and subsequently tested them in an instrumental procedure in which actions led to presentation of the Pavlovian cue. Central nucleus lesioned animals displayed a deficit in the nonspecific suppression of instrumental responding (conditioned suppression) produced by the cue, whereas basolateral amygdala lesioned animals exhibited a deficit in biasing instrumental choices away from an action that produced the cue (conditioned punishment). In another example, Corbit and Balleine, using a selective satiation procedure for instrumental actions that led to different rewards, demonstrated that central nucleus lesions (previously implicated in Pavlovian-instrumental transfer; Hall et al., 2001; Holland and Gallagher, 2003) selectively impaired general forms of Pavlovian-instrumental transfer but that specific forms were selectively impaired with basolateral amygdala lesions (Corbit and Balleine, 2005). Such dissociation is borne out in other paradigms. The central nucleus has been shown to be critical for contextual conditioning (Selden et al.,

1991), conditioned approach (Hitchcott and Phillips, 1998), and conditioned orienting (Holland et al., 2002a), whereas the basolateral amygdala has been shown to be critical for reinforcer revaluation (Balleine et al., 2003; Hatfield et al., 1996; Malkova et al., 1997), conditioned reinforcement (Cador et al., 1989; Hitchcott and Phillips, 1998), and second-order conditioning (Burns et al., 1993; Hatfield et al., 1996).

These and other results (Blair et al., 2005; Ostlund and Balleine, 2008; Wilensky et al., 2000) suggest that the basolateral amygdala encodes specific value-related outcome information, such as that modulated by satiety. The anatomical connections that may subserve this have been elucidated in a series of elegant experiments on conditioned potentiation of feeding. In this paradigm, Pavlovian cues paired with food when individuals were hungry can motivate sated animals to eat beyond satiety. Rats with lesions of the basolateral, but not central, amygdala do not show the characteristic potentiation of feeding normally seen when the Pavlovian cues are presented (Holland et al., 2001, 2002b). This effect depends on connectivity with hypothalamus and orbitomedial prefrontal cortex (Petrovich et al., 2002, 2005) but not striatum or lateral orbitofrontal cortex (McDannald et al., 2005). Indeed, a wealth of other experiments have confirmed the importance of amygdala-OFC connections in mediating the impact of outcome-specific value representations on choice (Baxter et al., 2000; Baxter and Browning, 2007; Ostlund and Balleine, 2007; Paton et al., 2006; Saddoris et al., 2005; Schoenbaum et al., 2003; Stalnaker et al., 2007).

Amygdala connectivity with nucleus accumbens mediates a number of other Pavlovian influences on action. First, autoshaping and higher-order conditioned approaches depend on the integrity of basolateral amygdala and nucleus accumbens and their interconnections (Parkinson et al., 2000, 2002; Setlow et al., 2002). This may be an important mediator of the Pavlovian impulsivity seen in paradigms such as negative automaintenance (Dayan et al., 2006; Williams and Williams, 1969). Second, lesions of the core and shell of the nucleus accumbens disrupt specific and general forms of Pavlovian-instrumental transfer, respectively (Corbit et al., 2001).

Decision Making in Humans

The extent to which behavioral and anatomical findings from rodents can be translated to humans (and primates) is an important and open issue, because experimental data (in decision-making tasks) on the latter are more scant. Human patients with amygdala damage are impaired in decision-making tasks involving risk and uncertainty, as are patients with ventromedial prefrontal damage (Bechara et al., 1999). Using fMRI, Hampton and colleagues have shown that patients with amygdala lesions have impaired outcome representations for instrumental choices in ventromedial prefrontal cortex (Hampton et al., 2007), an area known to be critical for learning action-outcome contingencies in instrumental learning (Bechara et al., 2000; Hampton et al., 2006; Kim et al., 2006), as it is in rats (Coutureau et al., 2000). Accordingly, the amygdala-medial prefrontal pathway may be a critical route by which stimulus-specific outcome information is integrated with more sophisticated, goal-directed actions.

Indeed, many animal results have parallels with human experiments (Delgado et al., 2006; Phelps and LeDoux, 2005). For instance, an amygdala contribution to human

Pavlovian-instrumental transfer has recently been reported in the context of an appetitive conditioning paradigm (Talmi et al., 2008). Amygdala and orbitofrontal cortex are both implicated in specific representations of outcome value in a similar manner to animals (Gottfried et al., 2003), and this circuit may underlie aspects of choice studied in behavioral economics. For example, both areas are involved in using previous experiences of regret to bias future decisions (regret avoidance); whereas the orbitofrontal cortex appears important for representing the negative motivational value of regret, the amygdala appears more specifically involved in biasing future decisions (i.e., learning) (Coricelli et al., 2005). And consistent with other parallels, the amygdala has been shown to have a central role in biasing choice in the framing effect to cause risk aversion in positive contexts (De Martino et al., 2006; Figure 3), and in economic transactions (selling objects) causing loss aversion (Weber et al., 2007).

The role of the amygdala further extends to other aspects of economic uncertainty. Humans, in general, have an aversion to selecting options to which the probabilities determining the outcomes are unknown (ambiguous), compared to options in which they are known (risk), even when the overall expected value of each is equivalent. By directly comparing choices made under risk or ambiguity, Hsu and colleagues (Hsu et al., 2005) have shown that amygdala activity predicts subjects' decisions to opt for less-ambiguous options. Intriguingly, lesions of the central nucleus of the amygdala in the rat appear to impair the increase in learning due to increases in cue-outcome associability (uncertainty) (Holland and Gallagher, 1993). Associability, being theoretically aligned to ambiguity by the fact that both drive learning (in contrast to risk), is thought to control learning via the neuromodulators acetylcholine and norepinephrine (Yu and Dayan, 2005), midbrain sources of which (nucleus basalis and locus coeruleus, respectively) both receive substantial input from the central nucleus.

A Role in Social Decision Making?

One of the most notable findings from human fMRI studies is the exquisite sensitivity of the amygdala to motivational information provided by faces, including to complex social information such as moral status, trust, and suspicion (Adolphs et al., 1998; Adolphs and Spezio, 2006; Calder and Young, 2005; Moll et al., 2005; Singer et al., 2004; Winston et al., 2002). How such rich motivational information can be used to influence choice, both in terms of relatively basic hardwired responses and integration with more goal-directed social decision making, is little understood, but one possibility is that Pavlovian mechanisms are involved. Choice in social interaction harbors a level of complexity that makes it unique among natural decision-making problems, because outcome probabilities depend on the unobservable internal state of the other individual, which incorporates their motives (intentions). Because most interactions are repeated, optimal learning requires subjects to generate a model of another individuals' behavior, and their model of our behavior, and so on. These iteratively nested levels of complexity render many social decision-making problems computationally intractable (Lee, 2006).

Pavlovian learning mechanisms may offer help. First, by invoking inherent prosocial tendencies (e.g., empathy and various

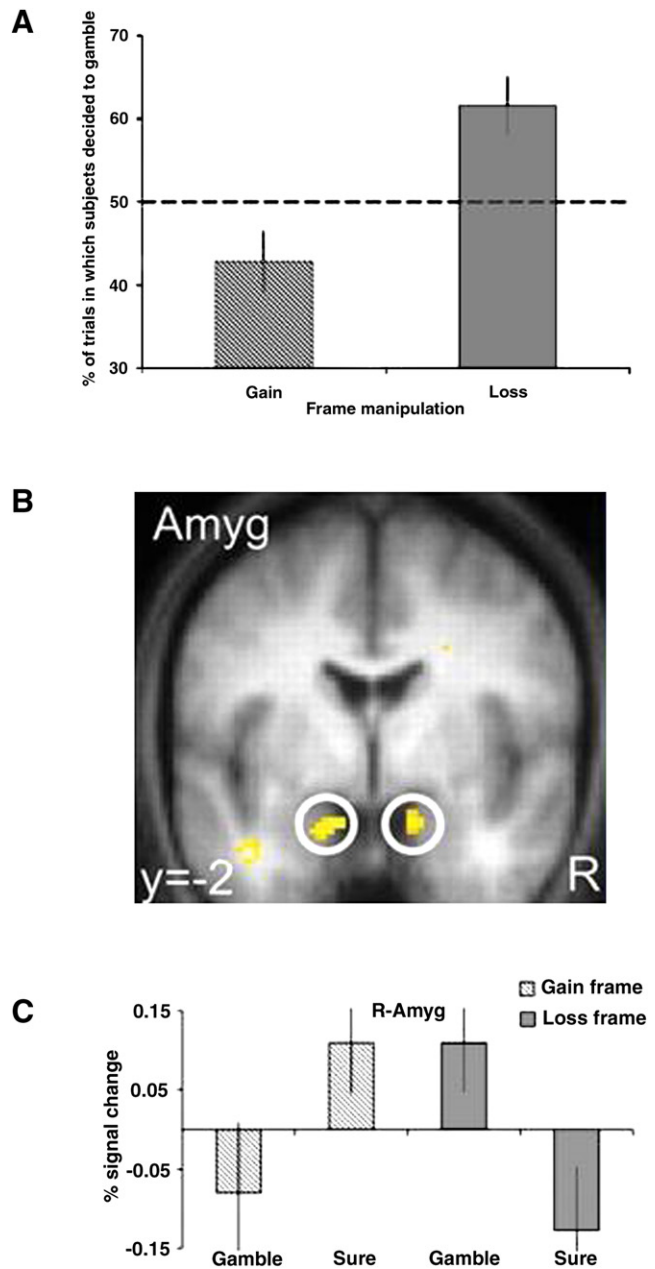


Figure 3. The Framing Effect and the Amygdala

Reproduced from De Martino et al. (2006).

(A) Behavioral frame biases. Subjects chose between a risky gamble and a sure option in a forced-choice paradigm in which each option had the same expected value, but the sure option was presented in either a positive frame (in terms of winning) or a negative frame (in terms of losing). Subjects bias their choices toward gambling in the “loss” frame, consistent with the well-described frame effect, in which negative frames cause people to become more risk seeking. Error bars denote SEM.

(B) BOLD responses. Activity in the amygdala strongly correlates with the direction of the frame bias (choice × frame interaction) at the time of choice.

(C) Amygdala activity. BOLD signal change as a function of choice and frame, displaying how activity follows the behavioral direction of the frame bias. Error bars denote SEM.

forms of altruism), Pavlovian mechanisms may prime reciprocity, to the mutual advantage of cooperators (Seymour et al., 2007). Second, associative value learning mechanisms have the capacity to associate positive and negative outcomes across individuals and circumstances, and estimates of trustworthiness provide a way of generalizing prosocial tendencies in other individuals and across different types of social interaction (Axelrod and Hamilton, 1981; King-Casas et al., 2005; Trivers, 1971). As an approximate inference about a hidden variable, namely cooperative reciprocity, in the brain of others, it is a key determinant of future outcomes that may obviate the requirement to model precisely the complexity inherent in repeated social interactions (Kraives and Kraives, 1993). Indeed, simple associative learning models have proved remarkably good at predicting behavior in human game theoretic tasks (Erev and Roth, 1998, 2007) and that the amygdala may utilize such approximations is hinted at by very recent studies that have manipulated trust using oxytocin (Baumgartner et al., 2008).

Conclusions

Clearly, there are several distinct mechanisms by which the amygdala plays a key role not just in simple conditioning but in complex decision making. Through Pavlovian learning, the amygdala can evoke conditioned responses that reflect an evolutionarily acquired action set capable of exerting a dominant effect on choice. Second, amygdala-based Pavlovian values are exploited by instrumental (habit-based and goal-directed) learning mechanisms in specific ways, through connectivity with other brain regions such as the striatum and prefrontal cortex.

We have argued that such Pavlovian integration is a theoretically reasonable strategy for improving and optimizing choice outcomes. How this relates to traditional notions of emotion is an open question, because definitions of emotion are often characteristically vague. Whereas there may be much more to emotion than that captured by innate values and responses and their acquisition in Pavlovian conditioning, most modern accounts of emotion contain these processes as a central theme (Dolan, 2002; LeDoux, 2000a; Rolls, 1998). Thus, the popular notion that emotional mechanisms are irrational may be ill-conceived, arising as an artifact of the fact that it is only when the influence of emotional (Pavlovian) mechanisms is suboptimal are we prone to be aware of their operation.

Lastly, there are notable parallels between the sorts of decision-making tasks well-studied in behavioral economics and the paradigms used by learning theorists, whose subjects are often nonhuman. Not only can neuroscientists learn much from the ingenious paradigms of behavioral economists, but the latter may benefit from the insights into the basic structure of decision making, and its subtle complexities, yielded by neuroscience.

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