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CITATION

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A revised view of the amygdala, its relationship with the prefrontal cortex (PFC), and its role in intelligent human decision-making is proposed. Based on recent findings, we present a framework in which the amygdala plays a central role in the value computations that determine which goals are worth pursuing, while the PFC plays a central role in generating and evaluating possible action plans to realize these goals. We suggest that the amygdala and PFC continuously work together during decision-making and goal pursuit as individuals compute and recompute the value and likelihood of different goals while interacting with a dynamic world. Once seen as chiefly involved in simple stimulus–outcome associative learning, the amygdala is shown to play a sophisticated role in human decision-making by contributing to the moment-by-moment integration of multiple costs and benefits to determine optimal choices. We discuss implications of the framework for brain development, emotion regulation, intelligence, and psychopathology.

Keywords: value, motivation, reinforcement learning, goal, emotion

This article is about the amygdala and, in particular, how its functions and its interactions with the prefrontal cortex (PFC) play a key role in intelligent decision-making. Historically, the amygdala has been seen as playing a secondary, perhaps even subservient, role to the PFC. We instead propose that they play complementary roles in constructing intelligent decisions. Specifically, we propose that the amygdala plays a central role in the value computations that determine which goals are worth pursuing, while the PFC plays a central role in simulating and evaluating possible action plans to realize these goals.

Over the past 25 years, the neuroscience of value-based decision-making has made tremendous progress in discovering the contributions of many subcortical and cortical brain regions to decision-related processes (e.g., Averbeck & Costa, 2017; Bartra et al., 2013; Bechara & Damasio, 2005; Damasio, 1994; Haber & Knutson, 2010; Rangel et al., 2008; Rushworth et al., 2011; Sharpe & Schoenbaum, 2016). Although this work has emphasized the idea that many regions work together to support the formation of intelligent decisions, much of this research has emphasized the PFC as the "jewel in the crown" so to speak. Specifically, much of the existing research contains implicit or explicit notions of a hierarchy in which many lower-level regions feed "raw material" to the PFC (particularly the ventromedial PFC/orbitofrontal cortex), which then computes the value of different choices and guides decisions.

There appear to be at least two reasons for this emphasis on the PFC, both of which emphasize the sophistication, and hence the uniqueness, of PFC functions. Yet, we will present evidence that the PFC is not unique in these abilities and that the amygdala is entirely capable of performing similarly sophisticated functions.

First, the PFC is believed to serve as a domain-general value-computing system that maps raw inputs onto a "common currency" space and allows different options to be directly compared (Ballesta et al., 2020; Behrens et al., 2008; Juechems et al., 2019; Levy & Glimcher, 2012; O'Doherty, 2011; Padoa-Schioppa & Conen, 2017; Rich & Wallis, 2016; Rustichini & Padoa-Schioppa, 2015; Strait et al., 2014; Yamada et al., 2018). Thus, according to this idea, the value signals and comparison process supported by the PFC are uniquely relevant for guiding choice.

Second, reinforcement learning (RL) models, which have become increasingly popular, have long emphasized the PFC as a primary neural substrate underlying sophisticated "model-based" value computations (e.g., Daw et al., 2005; Dolan & Dayan, 2013; Gläscher et al., 2010; Hampton et al., 2006; Holroyd & Verguts, 2021; Jones et al., 2012; Smittenaar et al., 2013). The implication is that these sophisticated model-based calculations of the PFC are able to account for intelligent decision-making.

However, a variety of evidence suggests that the PFC is not unique in either of these regards. In particular, we will review evidence demonstrating (a) that the amygdala also supports integrative common currency value signals that predict choice and (b) that amygdala activity meets the criteria for sophisticated model-based value computations. In fact, amygdala computations are sufficiently complex that they contribute to tasks traditionally defined as "cognitive," such as working memory and attention (e.g., Adolphs, 2010; Peck et al., 2013; Pessoa, 2008, 2010; Schaefer et al., 2006; Todd et al., 2012).

These data challenge the idea that the PFC is the chief integrative center that steers goal-related decisions.

If the amygdala and PFC are not distinguished by the sophistication of their computations and do not have a hierarchical relationship, what then are their relative roles in guiding intelligent decisions? The purpose of this article is to present the view that the amygdala and PFC play complementary roles with the amygdala being preferentially involved in model-based value computations that determine which goals are worth pursuing in order to satisfy current and future needs (e.g., the need for food or positive social relationships) and the PFC being preferentially involved in model-based simulations of goal-relevant action plans and in evaluating those plans in terms of likely effectiveness and cost. Furthermore, we suggest that decision-making (and goal-directed behavior in general) involves continuous interactions between the amygdala and PFC which allow for potentially valuable goal states to become coupled with action plans.

Our framework builds on and extends prior models that have pointed to the role of the amygdala in adaptive value computations that influence decision-making (e.g., Adolphs & Anderson, 2018; Averbeck & Costa, 2017; Cunningham & Brosch, 2012; Grabenhorst & Schultz, 2021; Janak & Tye, 2015; Morrison & Salzman, 2010; Pessoa, 2010; Seymour & Dolan, 2008; Sharpe & Schoenbaum, 2016; Wassum & Izquierdo, 2015) and models that have pointed to the cooperative nature of amygdala–PFC interactions (e.g., Baxter & Murray, 2002; Bechara et al., 1999; Gaffan et al., 1993; Gangopadhyay et al., 2021; Lichtenberg et al., 2017; Morrison & Salzman, 2010; Sharpe & Schoenbaum, 2016). However, given these important theoretical developments, why has much prominent work continued to portray the PFC as having the dominant influence in governing decisions? One possibility is that this is because there has yet to be a coherent narrative that ties together all of the available evidence, that explicitly attributes a sophisticated model-based value-computing role to the amygdala, and that describes how these computations may differ from, and work in collaboration with, those of the PFC in the service of decision-making. In line with this, Averbeck and Costa (2017) point out that the nature of amygdala value computations has not been well incorporated into prevalent models of decision-making.

We believe that our perspective is unique in explicitly suggesting that, like the PFC, the amygdala is involved in *model-based* value computations that are integrative, forward looking (i.e., sensitive to future consequences), and flexible (i.e., can rapidly adapt without requiring extensive corrective feedback). According to this perspective, the amygdala and PFC operate in parallel and perform complementary functions that co-create intelligent decisions. The key idea, as we have suggested, is that the amygdala is closely aligned with the ultimate motivations that drive behavior (e.g., the desire to be well fed, liked by others, and perceived as smart and competent), while the PFC is closely aligned with cognitive and action-related functions that support the means by which those ultimate goals are achieved. These means represented by the PFC may be concrete (e.g., walking from place A to B) or highly abstract (e.g., regulating thoughts in order to feel better).

To support this argument, we highlight evidence that the amygdala is anatomically positioned to operate as an integrative hub that can combine information about current needs (Baxter & Murray, 2002; Douglass et al., 2017; Gangopadhyay et al., 2021; Gothard, 2020; Hu et al., 2021; Izquierdo & Murray, 2007; Kwon et al., 2021) with sensory and contextual information (Cunningham & Brosch, 2012; Prévost et al., 2013; Saez et al., 2015) and the possible future consequences of choices (Ghods-Sharifi et al., 2009; Hernádi et al., 2015; Winstanley et al., 2004; Zangemeister et al., 2016). Furthermore, we draw upon evidence that many PFC regions are highly connected to the motor system (Passingham & Wise, 2012; Picard & Strick, 1996; Vogt, 2009; Yeterian et al., 2012), contain a somatotopic organization (Dum & Strick, 1991; Jezzini et al., 2012; Procyk et al., 2016; Vogt, 2009), are sensitive to the costs and benefits of possible actions (Rushworth et al., 2011; Shackman et al., 2011; Shenhav et al., 2013; Shima & Tanji, 1998; Touroutoglou et al., 2020), and show robust engagement during the planning and execution of specific actions (Bunge et al., 2003; Dixon et al., 2014; Gerlach et al., 2014; Tanji & Hoshi, 2001; Vogt, 2016; Zangemeister et al., 2016).

Scope of the Current Article

Based on a systematic review of the literature, our goal is to present a framework for how the amygdala and amygdala–PFC interactions contribute to value-based decision-making in humans. The amygdala and PFC are, of course, not monolithic or isolated entities. In fact, each is composed of numerous subregions or nuclei and even more localized cell types that each has specific electrophysiological properties and connectivity patterns (e.g., Allen et al., 2017; Ciocchi et al., 2010; Haubensak et al., 2010; Hong et al., 2014; Tye et al., 2011; Wang et al., 2018; for reviews, see Duvarci & Pare, 2014; Janak & Tye, 2015). However, in keeping with our goal of providing an overarching account of how the amygdala and PFC co-create intelligent decisions, our primary task is to characterize the "overall" functions of the amygdala and PFC which may emerge from the collective interactions of their specific subregions, cell types, and microcircuits according to multiscale network-based principles (e.g., see Wilson et al., 2010).

Our focus is on human decision-making and therefore most of the human studies that we review employed functional magnetic resonance imaging (fMRI) or examined people with lesions; few studies recorded single-unit activity. While these human studies offer critical insights, they also have limitations—fMRI is an indirect measure of neural activity that has limited temporal resolution, and human lesion studies may involve heterogeneous causes, varying amounts of time since the lesion, and different spatial distributions (i.e., lesions may encompass regions beyond the amygdala or encompass different sets of PFC subregions).

For these reasons, we also review findings from non-human animals (primates and rodents)—species that have a clearly defined amygdala and PFC—to support our case. These studies used either single-unit recordings or acute disruption (via lesions, optogenetic stimulation, or pharmacological inactivation) to directly examine neural activity patterns and their functional consequences. Of course, these data are also limited in that there are important behavioral and neurobiological differences between humans and non-human animals. Therefore, combining human and non-human animal findings provides a broad picture of how the amygdala and amygdala–PFC interactions contribute to value-based decision-making.

In the following sections, we first provide an in-depth analysis of studies showing that the amygdala demonstrates sophisticated computational properties and promotes intelligent decisions.

This is followed by an overview of the complementary role of the PFC in action generation, evaluation, and planning, focusing on the contributions of several PFC subregions. We then bring these pieces together by addressing amygdala–PFC interactions in decision-making and during goal pursuit. In order to stimulate future research on the contributions of the amygdala to decision-making, we also consider the way in which the amygdala's role differs from the functions of several other motivation-related brain regions. Finally, we conclude with a discussion of the implications of this revised understanding of amygdala–PFC interactions in intelligent decision-making for such topics as intelligence, emotion regulation, and psychopathology.

Properties of the Amygdala

Before providing evidence of the amygdala's involvement in intelligent decision-making, we first review findings suggesting that it possesses essential properties that enable it to play a central role in predicting the value of possible goal states. Specifically, below we provide evidence that the amygdala is characterized by:

i. Widely distributed anatomical connectivity, enabling it to receive and integrate a wide variety of need-relevant signals, and to send goal-relevant output to appropriate places.

ii. Flexible value-coding properties that could support intelligent goal-value computations.
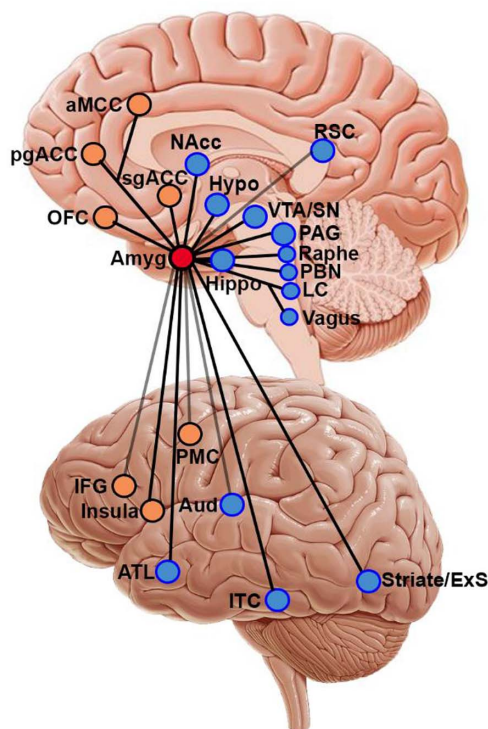
The Amygdala Is a Connectivity Hub

The amygdala is anatomically connected to widely distributed areas of the brain, making it well positioned to operate as a "hub" that can integrate diverse information and modulate other systems in accordance with goal values (Figure 1; Bickart et al., 2014; Pessoa, 2008). In particular, the amygdala is anatomically positioned to receive and integrate a variety of information relevant to goal-value computation, including information about current needs, situational context, prior experience, and high-level cognitive representations (e.g., related to possible future events).

While we will generally refer to "the amygdala" throughout the manuscript for simplicity, it is important to note that it is a heterogenous structure consisting of multiple distinct nuclei with different connectivity patterns (Duvarci & Pare, 2014; Janak & Tye, 2015; Pitkänen et al., 1997; Swanson & Petrovich, 1998). It is often subdivided into two major areas that encompass a large portion of the amygdala and many of its nuclei: (a) the basolateral amygdala (BLA) complex, consisting of the basal, basomedial, and lateral nuclei; and (b) the central amygdala (CeA), consisting of primarily the central nucleus, which contains medial and lateral subdivisions (Janak & Tye, 2015; LeDoux, 2000; McDonald, 1998). We refer to these two subdivisions when describing connectivity patterns and functions of the amygdala, but acknowledge that the picture is more complex and will ultimately require a thorough understanding of all amygdala nuclei. With few exceptions, the connections reviewed below are bidirectional.

Figure 1

A Highly Simplified Illustration of the Anatomical Connections of the Amygdale

Note. It is important to keep in mind that individual nuclei have distinct connectivity patterns and that this figure is only a general summary. The amygdala has direct (monosynaptic) connections with widespread areas of the brain, positioning it as a connector "hub." These connections include sensory regions, various parts of the prefrontal cortex (orange nodes), brainstem and subcortical homeostatic regulatory regions, memory regions, and other cognitive regions (blue nodes). We highlight PFC regions in orange to demonstrate the widespread connectivity between the amygdala and PFC. Lower opacity lines reflect weak (but present) connections. ATL = anterior temporal lobe; aMCC = anterior midcingulate cortex; Aud = auditory cortex; ExS = extrastriate cortex; Hippo = hippocampus; Hypo = hypothalamus; IFG = inferior frontal gyrus; ITC = inferotemporal cortex; LC = locus coeruleus; NAcc = nucleus accumbens; OFC = orbitofrontal cortex; PAG = periaqueductal gray; PBN = parabrachial nucleus; pgACC = pregenual anterior cingulate cortex; PMC = premotor cortex; RSC = retrosplenial cortex; sgACC = subgenual anterior cingulate cortex; VTA/SN = ventral tegmental area/substantia nigra; PFC = prefrontal cortex. See the online article for the color version of this figure.

Sensory Connections

The amygdala is richly connected with all sensory modalities, suggesting it has access to detailed representations of "what is currently happening" (Aggleton et al., 1980; Amaral & Price, 1984; Ghashghaei & Barbas, 2002; McDonald, 1998; Price, 2003). Furthermore, the amygdala projects back to each of these areas, providing a route by which it can modulate sensory processing to enhance the representation of goal-relevant events (Anderson & Phelps, 2001; Pessoa, 2010; Todd et al., 2012; Vuilleumier, 2005). In general, sensory connections (especially visual, auditory,

and somatosensory) are robust for the BLA but weak or absent for the CeA (McDonald, 1998; Price, 2003).

Connections With Memory Regions

The amygdala also has robust connections with a variety of memory-related regions (hippocampus, parahippocampal gyrus, perirhinal and entorhinal cortices, retrosplenial cortex, ventromedial PFC; Aggleton et al., 1980; McDonald, 1998; Parvizi et al., 2006) that are involved in constructing spatial, autobiographical, and schema-based models of the world (Behrens et al., 2018; Gilboa & Marlatte, 2017; van Kesteren et al., 2012). Input from these regions to the amygdala may contextualize sensory input based on prior experience and supply information about simulated future events, thereby endowing the amygdala with information that can support model-based value computations.

Need-Relevant (Homeostatic) Connections

The amygdala also has access to need-relevant interoceptive signals (e.g., pleasant and nociceptive signals related to hunger, thirst, temperature, affective touch; Craig, 2002; Johansen et al., 2010; Sternson & Eiselt, 2017) via monosynaptic connections with the insula, hypothalamus, periaqueductal gray (PAG), bed nucleus of the stria terminalis, parabrachial nucleus, nucleus of the solitary tract, and vagus nerve (Aggleton et al., 1980; LeDoux, 2000; McDonald, 1998; Price, 2003; Price & Amaral, 1981). The amygdala also projects to the ventral striatum (VS) and is well connected to nuclei that control the release of major neuromodulators (chemicals that modulate brain function often based on motivationally significant information), including the ventral tegmental area/substantia nigra (VTA/SN; dopamine), dorsal raphe nucleus (serotonin); locus coeruleus (norepinephrine), and basal nucleus of Meynert (acetylcholine; Aggleton et al., 1980; McDonald, 1998; Price & Amaral, 1981). Some of these homeostatic connections are stronger for the CeA, but they are also present for the BLA (Price, 2003). Thus, by combining homeostatic (interoceptive) inputs with a rich stream of exteroceptive sensory data and memory-related (model-based) information, the amygdala is well positioned to contribute to the process of determining the goal relevance or value of ongoing events and contributing to decisions about which goals to pursue. Moreover, projections back to these regions would allow the amygdala to widely influence information processing based on current goal values.

PFC Connections

The amygdala has access to cognitive and action-related information via connections with PFC regions including the orbitofrontal cortex (OFC), pregenual and subgenual anterior cingulate cortex (ACC), anterior midcingulate cortex (aMCC), and insula (Aggleton et al., 1980; Amaral & Price, 1984; Carmichael & Price, 1995; Ghashghaei & Barbas, 2002; Johansen-Berg et al., 2008; McDonald, 1998; Porrino et al., 1981; Price, 2003). The amygdala also has weak connections with the premotor cortex and inferior frontal gyrus (Amaral & Price, 1984). Although the amygdala is weakly connected with the lateral PFC (Ghashghaei & Barbas, 2002)—a key region involved in the executive control of behavior—it may communicate indirectly with this region via intermediary PFC regions (e.g., OFC, cingulate cortex, insula) or

the thalamus. Altogether, these PFC connections may provide a route by which goal-value computation can become coupled with cognitive activity including the simulation of possible action plans. PFC connections are generally stronger for the BLA compared to the CeA (Ghashghaei & Barbas, 2002).

Connections With the Thalamus

In addition to direct connections between the amygdala and the PFC, these regions are indirectly connected to each other via the mediodorsal thalamus (Aggleton & Mishkin, 1984; Porrino et al., 1981)—a pathway that contributes to value-based learning and choice (Gaffan et al., 1993; Gaffan & Murray, 1990; Murray & Rudebeck, 2013). Evidence suggests that the mediodorsal thalamus does not simply amplify amygdala or PFC activity, but may promote plasticity (Baxter, 2013) in a way that allows models of the world used by the amygdala and PFC to be updated. Thus, these connections with the thalamus may further endow the amygdala with information needed to support sophisticated model-based value computations.

Summary of Anatomical Connectivity

To summarize, the amygdala's input connections provide information about a wide range of sensory and need-relevant signals conveying what is currently happening in the internal and external environment. These connections would enable the amygdala to contribute to the process of determining the current value of possible goal states. The amygdala's widespread output connections may allow it to influence and possibly coordinate brain-wide dynamics involving multiple systems (perceptual, autonomic, action, cognitive). Consistent with this, pharmacological inactivation of the amygdala disrupts communication throughout the global brain landscape, resulting in weaker communication between PFC regions (e.g., orbital and medial PFC), between limbic regions, and between limbic and PFC regions (Grayson et al., 2016).

These results suggest that the amygdala may serve as a glue that binds together large-scale neural circuits. Broadly in line with this, "resting state" functional connectivity studies with humans have demonstrated that fluctuations in amygdala activity are coupled to activity fluctuations in large-scale brain networks involved in interoception, memory, attention, and social cognition (e.g., the amygdala couples with regions associated with the salience network, dorsal attention network, and default mode network; Bickart et al., 2014; Gabard-Durnam et al., 2014; Kerestes et al., 2017; Kleckner et al., 2017; Roy et al., 2009; Seeley et al., 2007; Sylvester et al., 2020).

Flexible Value-Coding Properties

Before addressing the contribution of the amygdala to goal-value computations and to making decisions between goals, we first note some of the general properties of amygdala value coding that have been observed across a range of tasks.

A variety of evidence suggests that the amygdala is centrally involved in the generation of valence—the motivational value that colors an event as good or bad and has the effect of mobilizing attention, cognitive resources, and action planning systems. Studies that have presented individuals with rewarding or aversive outcomes have identified intermingled populations of valence-specific

neurons in the amygdala—populations that have distinct genetic profiles and anatomical projections (e.g., Belova et al., 2008; Lee et al., 2016; Paton et al., 2006; Schoenbaum et al., 1999; Shabel & Janak, 2009; reviewed in Janak & Tye, 2015; Morrison & Salzman, 2010; O'Neill et al., 2018; Pignatelli & Beyeler, 2019). Although some neurons respond to both positive and negative outcomes and may therefore encode a salience/intensity signal (e.g., Belova et al., 2007, 2008; Shabel & Janak, 2009), a large proportion of neurons selectively respond to positive or negative outcomes. These valence-coding neurons signal the value of virtually any goal-relevant stimuli (Adolphs, 2010; Ambroggi et al., 2008; Anderson et al., 2003; Baxter & Murray, 2002; Belova et al., 2008; Büchel & Dolan, 2000; Davis et al., 2010; Gottfried et al., 2003; Holland & Gallagher, 2004; Hu et al., 2021; Kwon et al., 2021; LeDoux, 2000; Munuera et al., 2018; Paton et al., 2006; Sescousse et al., 2013; Schoenbaum et al., 1998; Sharpe & Schoenbaum, 2016; Tye et al., 2008). In fact, amygdala lesions result in profound impairments that render individuals "blind" to the value of events (Weiskrantz, 1956).

Importantly, there is flexibility in how events are tagged with value by the amygdala. It is not the case that once an event is associated with negative value, the amygdala will rigidly signal negative value every time that event is encountered in the future. Instead, signals encoded by the amygdala flexibly adapt to the current value of events, which may change depending on internal context (e.g., current needs) or external context. For example, the amygdala plays a necessary role in the ability to update the value of particular foods based on current levels of hunger (Baxter & Murray, 2002; Gottfried et al., 2003; Hatfield et al., 1996; Izquierdo & Murray, 2007; Johnson et al., 2009). Furthermore, the same stimulus can evoke different patterns of activity in the amygdala depending on changing external context such as task instructions (Cunningham & Brosch, 2012).

Amygdala Contributions to Intelligent Decision-Making

Turning now to decision-making, an intelligent decision maker should demonstrate a number of important characteristics. Among other things, they should take the future consequences of choices into account; should balance the desirability of choice options with their probability of realization; should be willing to invest high levels of effort when it will result in highly desired outcome; and should consider the social context in order to learn from others and make decisions that respect the goals of others. In the following sections, we show that empirical evidence substantiates our proposal that the amygdala contributes to intelligent decision-making by comparing amygdala function to these characteristics of an intelligent decision maker. We further examine the evidence that amygdala activity predicts the choices that individuals make in decision-making tasks; that amygdala activity preferentially reflects online computations of value rather than passive retrieval of stimulus–outcome associations; and that the amygdala is more engaged when forming goals than when actions are being taken to realize them.

Consideration of Future Consequences

Intelligent decision-making requires consideration of not only the immediate implications of a choice, but also future consequences. For example, it is generally thought that choosing to save some

money (rather than immediately spend it all) is an intelligent decision because the saved money can accumulate interest and be available to serve future needs. Future events may initially be represented by the PFC (through its powers of event simulation); however, we propose that the amygdala plays a key role in tagging these representations with value based on current needs.

In one study designed to test economic savings behavior (Zangemeister et al., 2016), human participants fasted (no food or drink) for several hours and then made decisions about how long to save a food reward (a vanilla-flavored dairy drink) before consuming it. The longer they chose to save the reward before consuming it, the more it accumulated according to the "interest rate" on a given trial. It was, therefore, especially beneficial to save the reward on high-interest rate trials which resulted in a large payoff later. Participants first formed a savings goal on each trial (i.e., they decided how long they planned on saving the reward) and then indicated via button press every ~13 s whether they wanted to continue saving the reward or consume it. Participants could therefore choose to consume the reward at any point, making this an active decision process throughout the duration of the trial.

Notably, the magnitude of amygdala activation at the time of the initial decision (forming the savings goal) predicted both the length of time that participants chose to save the reward and the value of the saved reward given the interest rate on that trial (Zangemeister et al., 2016). Specifically, greater amygdala activation was associated with saving for a longer period of time, especially on high-interest rate trials when it was especially beneficial to do so (Zangemeister et al., 2016). Amygdala activation began prior to the execution of goal-directed actions (button presses) and then was sustained until reward consumption several minutes later, suggesting that it was specifically involved in computing the value of the savings goal and in the continued signaling of that goal until it was achieved. Thus, amygdala activity was future-oriented and sensitive to contextual information (the current interest rate), and predicted participants' choice on each trial. Using a similar task with monkeys, the authors again found that amygdala activity (localized to both the BLA and CeA) reflected the value of the internally generated savings goal and predicted savings behavior (Grabenhorst et al., 2016; Hernádi et al., 2015).

If the amygdala is critical for guiding decision-making based on future consequences, then lesions should make individuals more impulsive. Consistent with this, rats with BLA lesions are more likely than controls to choose a smaller, immediate reward over a larger but delayed reward (Winstanley et al., 2004; see also Ghods-Sharifi et al., 2009). Thus, empirical data suggest that the amygdala (alongside other regions such as the PFC) may contribute to intelligent decisions by enhancing the salience of future (in addition to immediate) consequences of choices, and in some cases, *overcoming impulsive decisions* by promoting a willingness to forgo an immediate reward if it means that waiting will result in a larger payoff.

Balancing the Desirability of Choice Options With Their Probability of Realization

In real-world situations, various outcomes are rarely guaranteed to occur. It is often the case that a choice will lead to one outcome or another with some probability. An intelligent decision maker should effectively integrate outcome magnitude and probability and choose

options associated with higher expected net value. In other words, they should not be swayed by outcome probability or magnitude information alone.

The Iowa Gambling Task is a classic measure of decision-making involving uncertainty that has been widely used to probe the effect of brain lesions in humans (Bechara & Damasio, 2005). In this task, individuals pick from decks of cards that offer varying rewards and punishments. Unbeknownst initially to participants, some decks offer large rewards on some occasions but even larger losses on other occasions and are therefore disadvantageous over the long run, while other decks offer small rewards on some occasions but even smaller losses on other occasions and are therefore advantageous over the long run. Although the correct choices are initially uncertain, control participants learn quickly to select primarily from the advantageous decks by integrating information about rewards and losses over time into an overall value for each deck. In contrast, humans with amygdala damage preferentially select from the disadvantageous decks across the entire task and fail to generate typical anticipatory physiological signals prior to risky choices (Bechara et al., 1999). Studies using other paradigms have similarly shown that individuals with amygdala damage do not integrate outcomes and probabilities in the same way as to control participants (De Martino et al., 2010). Moreover, in some cases, amygdala lesions in primates induce a more severe deficit in probabilistic choice tasks than lesions of other parts of the motivation system such as the VS (Costa et al., 2016).

Even when a potential loss is removed from the equation, individuals with amygdala lesions still cannot properly integrate reward magnitude and probability. For example, when presented with two reward options that differ in probability, humans with amygdala damage are more likely than controls to choose disadvantageous (objectively lower value) options (Weller et al., 2007). However, amygdala damage does not strictly lead to an increase in risky decisions. One study had rats choose between a guaranteed small reward and an uncertain (50% probability) large reward and found that animals with BLA lesions were more likely than controls to choose the certain/low-reward option (Ghods-Sharifi et al., 2009). Notably, this was objectively the lower value option across trials.

Thus, amygdala lesions can lead to different patterns of choices—sometimes biasing decisions toward the low but certain-reward option and sometimes biasing choices toward the high but risky reward option (Bechara et al., 1999; Costa et al., 2016; De Martino et al., 2010; Ghods-Sharifi et al., 2009; Weller et al., 2007; see discussion in Pessoa, 2010). Importantly, there is no contradiction, because in these studies amygdala lesions consistently led to suboptimal choices from a net-value perspective, presumably from a failure to integrate the relevant information within a given task (Pessoa, 2010). In line with these laboratory findings, patients with amygdala damage tend to make poor decisions in everyday life, suggesting that the laboratory task may capture an important element of decision-making (Bechara et al., 1999). Thus, existing evidence suggests that the amygdala supports intelligent decision-making by contributing to the ability to optimally integrate information about the desirability and probability of choice options (for related neuroimaging evidence see also Hsu et al., 2005). Individuals with orbitofrontal/ventromedial PFC damage also demonstrate aberrant decisions in gambling tasks, suggesting that the amygdala and PFC work together to promote adaptive decisions (Bechara & Damasio, 2005; Gupta et al., 2011).

Incorporating Effort Into Goal-Value Computations

The overall value of a goal is not just a function of the amount of reward it promises, but also depends on the amount of effort that must be invested in the actions that are required to realize the goal. Effort can factor into the computation of goal values in different ways (Dweck, 1999; Inzlicht et al., 2018). In thinking about what it means to make intelligent decisions, we often picture individuals who are willing to invest considerable effort to achieve highly desired outcomes, rather than simply settle for small rewards that can be achieved with little effort. Thus, if the amygdala contributes to intelligent decision-making, its activity should reflect the net value of goals (accounting for the effort required to achieve them) and bias decisions toward high-effort choices when they will result in a larger payoff than a low-effort option.

To look for brain regions that may integrate reward magnitude and required effort, Chong et al. (2017) had human participants perform a target detection task that varied in the amount of effort required (the frequency of shifting attention to detect target stimuli) and the monetary reward that could be earned. After learning the task, participants were presented with choices between performing the low- or high-effort version of the task and receiving various amounts of reward. To eliminate fatigue as a factor, participants made all of their choices up front and then performed a random subset of their choices at the end of the experiment. Using a computational modeling approach, the authors found that participants' choices reflected a combination of effort and reward magnitude (Chong et al., 2017). The authors reasoned that if a brain region contributes to decision-making in this task, it may do so by encoding the difference in net value between the two presented options. The results demonstrated that amygdala activation correlated with the difference in net value between the two options at the time of the decision period on each trial and not simply the difference in payoff or the difference in the effort required (i.e., it encoded the integration of the two variables). Specifically, greater amygdala activity was associated with a larger difference in net value between options and therefore reflected the overall value of choice options, by taking into account the required effort to achieve them.

Lesion studies have also provided evidence that the amygdala contributes to the integration of rewards and effort and promotes a willingness to invest more effort for a larger payoff. In these studies, rodents were presented with a choice between a low-value option that could be obtained with little effort, and a high-value option that could be obtained only by exerting considerable effort. Lesioning or inactivating the BLA reduced the animals' tendency to choose the high-effort/large-reward option over the low-effort/small-reward option (Ghods-Sharifi et al., 2009; Hosking et al., 2014). Furthermore, in the absence of an intact amygdala, animals became significantly slower to make a choice (Hosking et al., 2014). These findings suggest that without an amygdala, animals have difficulty integrating effort and reward magnitude into an overall value estimate and are less willing to invest effort to obtain a large payoff.

Notably, a variety of findings suggest that effort costs may be initially computed by parts of the PFC and striatum and involve dopamine (Chong et al., 2017; Croxson et al., 2009; Hamid et al., 2016; Jurado-Parras et al., 2020; Salamone & Correa, 2012; Westbrook et al., 2020). This information may then be sent to the amygdala where it can influence goal values. Thus, the key point is not that the amygdala computes all variables that are relevant to

determining the value of goals, but that it receives and integrates a variety of information that can influence value signals in a manner that promotes intelligent decisions. Several issues require clarity in future work, including the extent to which the amygdala contributes to cognitive versus physical effort-based decision-making (Chong et al., 2017; Ghods-Sharifi et al., 2009; Hosking et al., 2014) and the extent to which the default tendencies of the animals impact the way in which amygdala lesions alter effort-based decision-making (Hosking et al., 2014).

Sensitivity to Social Context

Intelligent decision-making often requires that individuals take into account their social context. In some cases, it is useful to observe others' actions and resulting outcomes and then copy their successful behaviors in order to more efficiently acquire beneficial outcomes for oneself. In other cases, it is useful to consider how various choices may impact one's relationships with others. For example, it is often intelligent to share resources with others because of the long-term benefits of having social partners who may reciprocate when they have access to resources or who may offer protection in times of conflict. Recent studies have demonstrated that the amygdala is exquisitely sensitive to social context during decision-making, consistent with prior observations that this region encodes a variety of social variables (e.g., facial expressions and the status of others; Adolphs, 2010; Gangopadhyay et al., 2021; Gothard, 2020; Kwon et al., 2021; Munuera et al., 2018).

One study recorded from amygdala neurons while monkeys performed an observational learning task (Grabenhorst et al., 2019). The monkeys learned to select a rewarded option faster when they first had the opportunity to observe another monkey's decisions with the same stimulus set compared to when they learned about a novel stimulus set, consistent with the idea that they took advantage of observational learning to improve their decisions. The fascinating finding was that amygdala neurons came to reflect the value of the options under consideration while the other monkey was making decisions and the more precise this observational value coding, the faster the monkey then made optimal choices when it was their turn to make decisions (Grabenhorst et al., 2019). Thus, amygdala neurons track important aspects of social context that facilitate intelligent decisions.

Another study used the Dictator game to demonstrate that the amygdala appears to be involved in steering decisions in ways that presumably serve to build or maintain positive social relationships (Chang et al., 2015). In this study, a decider monkey made decisions about how to split rewards between themselves and a recipient monkey. Critically, a significant number of BLA neurons with value-coding activity predicted the likelihood of making a prosocial decision (i.e., choosing to deliver the reward to both themselves and the recipient monkey vs. just themselves, or choosing to deliver the reward to the recipient monkey vs. neither getting a reward; Chang et al., 2015). Moreover, infusion of oxytocin into the BLA increased social gaze and the likelihood of making a prosocial decision. One interpretation is that the amygdala encodes the value of social partners and that oxytocin infusion enhanced the social value attributed to the other individual, thereby biasing attention and choices in a prosocial direction. Several studies have reported evidence that is broadly consistent with this social reinforcement idea (Hu et al., 2021; see also Hurlemann et al., 2010; Liu et al., 2019).

Do these amygdala value signals have meaningful consequences for social interactions? Lesion studies suggest that they do. Humans and nonhuman primates with amygdala lesions fail to display typical social behavior, show changes in social judgments and social attention, exhibit a decline in social status, and tend to become socially isolated (Adolphs et al., 1998; Baron-Cohen et al., 2000; Gothard, 2020; Kennedy & Adolphs, 2010; Kennedy et al., 2009; Stone et al., 2003). The amygdala may therefore play a key role (alongside other regions including the PFC) in decision-making by incorporating information about social context.

Activity That Predicts Choices

We have reviewed evidence that the amygdala integrates a variety of variables that impact decision-making. Influential models of decision-making suggest that the integration of relevant variables may be reflected in a subjective-value signal that ultimately guides the choices that individuals make. Although these models have generally suggested that it is the PFC (ventromedial PFC/OFC) that integrates various information into a subjective-value signal (e.g., Levy & Glimcher, 2012; Padoa-Schioppa, 2011), growing evidence suggests that the amygdala also contributes to a subjective-value signal that can guide choice.

Numerous studies have found that at the time of making a decision, amygdala activity does indeed correlate with a subjective-value signal (Chong et al., 2017; Gelskov et al., 2015; Grabenhorst et al., 2012; Jenison et al., 2011; Jezzini & Padoa-Schioppa, 2020; Zangemeister et al., 2016). In fact, a recent study of economic decision-making found the percentage of cells encoding the subjective value of the chosen option was higher in the amygdala (64%) compared to the OFC (41%)—the PFC region most closely tied to subjective-value computation (Jezzini & Padoa-Schioppa, 2020). Moreover, in the amygdala, this subjective-value signal was present quickly (~250 ms) after the choice options were presented and then was sustained throughout the rest of the trial, which included a delay period, a choice period during which a saccade was made to indicate the chosen option, and an outcome period when a juice reward was delivered. In contrast, in the OFC, this subjective-value signal only transiently appeared after the choice options were presented and then dissipated thereafter (Jezzini & Padoa-Schioppa, 2020). These findings suggest that the amygdala may have a more central role in subjective-value computation than previously appreciated.

Other studies have similarly found that amygdala activity predicts the choice that individuals ultimately make (Burgos-Robles et al., 2017; Chang et al., 2015; Grabenhorst et al., 2012, 2019). For example, in the economic savings task noted above, amygdala spiking activity recorded in monkeys predicted save versus spend (consume) choices with about 80% accuracy (Grabenhorst et al., 2012). In some of these neurons, there was a value-to-choice transition that resembled a decision process. In another study, Burgos-Robles et al. (2017) recorded activity in the BLA while rats were presented with distinct cues signaling a sucrose reward or a shock. The key trials involved presenting the cues simultaneously to investigate decision-making (choosing to approach or freeze) during goal conflicts. Using a machine learning classifier, the authors found that amygdala firing patterns were highly informative (~85% accuracy) regarding the decision that was ultimately made by the animal in the conflict trials (Burgos-Robles et al., 2017).

Finally, while amygdala lesions do not disrupt the presence of simple reward and punishment feedback signals in the PFC, they do diminish the presence of expected value signals in the PFC that are associated with behavioral choices (Hampton et al., 2007). This is consistent with the idea that at PFC value signals are at least partially dependent upon value information arriving from the amygdala.

These findings are consistent with the idea that the amygdala may play a key role in the computation of an integrated subjective-value signal that contributes to the choices that individuals make from trial to trial. This is not to say that the PFC plays no role in subjective-value computation. Rather, the key point is that the PFC is not the site at which an integrated subjective-value signal first appears. In other words, the amygdala and other regions do not simply supply the PFC with different types of raw material that are then transformed into a decision-guiding signal. It could be the case that a subjective-value signal is first computed in the amygdala and then passed to the PFC, or it could be the case that subjective-value signals emerge from the collective activity of several brain regions including the amygdala, PFC, and striatum.

Preferential Involvement in Active Decision-Making Versus Passive Encoding of Stimulus–Outcome Associations

To clearly favor an integrative value computation account of amygdala function, it would be useful to demonstrate that amygdala activity patterns are distinct when individuals are actively making decisions versus passively processing stimulus–outcome associations. Several studies have now reported evidence consistent with an integrative account (Chang et al., 2015; Grabenhorst et al., 2012, 2016, 2019).

In the study noted above on economic savings behavior (Grabenhorst et al., 2012, 2016), the authors compared a condition in which the monkey internally formed a savings goal with a condition in which the monkey saw the same visual cues (which were associated with the same outcomes), but did not need to make a decision because their behavior was dictated by an additional external cue that indicated the correct choice. Importantly, the authors found that goal-related activity in the amygdala disappeared when the monkey did not need to make an active decision (Grabenhorst et al., 2012, 2016).

In the study of social decision-making, described earlier, in which monkeys decided whether to share a food reward with another monkey (Chang et al., 2015), the authors found that mean firing rates of the decider monkey's BLA neurons correlated with the reward value of choice options for both themselves and the other monkey, but only on trials in which the monkey actively made a choice and not when the experimenter chose the outcome for the monkeys (Chang et al., 2015). This again reveals that value signals in the amygdala distinguish between active decisions and passively processing cue–outcome associations.

Finally, amygdala activity bears a closer resemblance to trial-by-trial variation in behavior than to the strict value signaled by cues, indicating that it more closely aligns with internally generated decision processes than passive cue–outcome processing (Lee et al., 2016). Together, these studies provide strong evidence that the amygdala may be more involved in actively computing values on the fly in service of decision-making than in signaling previously learned stimulus–outcome associations.

Preferential Involvement in Goal Formation Versus Action Planning

Our framework suggests that the amygdala is more involved in actively forming decisions about which goals to pursue than in orchestrating actions to achieve them. This idea can be tested by comparing amygdala activity during goal formation periods with its activity during action planning and execution periods. Several studies have done so, and have found evidence that supports our proposal: Amygdala engagement is stronger during goal formation than action planning/execution (e.g., Gerlach et al., 2014; Grabenhorst et al., 2016; Zangemeister et al., 2016).

Summary of the Amygdala's Role in Decision-Making

We reviewed a growing literature that unequivocally demonstrates amygdala involvement in many aspects of intelligent decision-making. Amygdala activity is sensitive to many costs and benefits, including the magnitude, timing, and probability of rewards, and the amount of effort that must be invested to achieve a goal. A consistent finding across studies is that the amygdala is preferentially engaged when the individual is actively making a decision rather than when the individual is passively processing stimulus–outcome values that are dictated by the experimenter. These findings are consistent with models suggesting that amygdala activity encodes a continuously evolving integrative "state value" signal—an overall assessment of the situation as being good or bad for the individual, given available actions (Belova et al., 2008; Paton et al., 2006; for a review, see Morrison & Salzman, 2010). This state value signal would play a central role in guiding decisions from moment to moment.

Importantly, we are not suggesting that the amygdala is entirely responsible for representing valued goals. Rather, the content of representations of possible future goal states may be supported by a distributed set of brain regions including sensory cortices, the hippocampus, and medial prefrontal and parietal regions (Buckner, 2010; Hassabis & Maguire, 2009; Schacter et al., 2007). The role of the amygdala in particular may be to assign value to these possible goal state representations based on their predicted impact on needs.

An implication of these findings is that the amygdala may in fact contribute to some functions traditionally considered more "cognitive" in nature. While the PFC has received the bulk of the attention with respect to executive functions, the data reviewed above suggest that the amygdala plays a key role in integrating various costs and benefits and that it influences whether an individual will choose to persist toward goals that require effort and the consideration of future outcomes—canonical elements of executive control. Furthermore, because the amygdala plays a role in the process of arbitrating between competing goals, it may well play a role in keeping an individual focused on a goal at hand and filtering out distraction related to alternative options. In line with this, empirical work has documented amygdala contributions to attention (Adolphs, 2010; Peck et al., 2013; Pessoa, 2010; Sennwald et al., 2016; Todd et al., 2012) and working memory (Schaefer et al., 2006). These findings are consistent with the notion that amygdala functions may

contribute to effective executive functioning. Thus, while the functions of the PFC most certainly align with conceptions of "executive functions," we suggest that some of the functions of the amygdala are also deserving of this label.

Finally, it is important to underscore that our goal is to highlight the underappreciated role of the amygdala in making intelligent decisions. It is not our intention to portray the amygdala as performing this role alone in a homuncular manner; rather, it acts in concert with many other brain regions. The idea that the amygdala plays a central role in adaptive value computations that guide decisions could be strengthened in future studies by using tasks in which it is necessary to dynamically compute and recompute goal values as various options become available or unavailable.

Amygdala Functions and Model-Based Reinforcement Learning

If the amygdala encodes an integrative state value signal, how might this value signal be computed? Answering this question may illuminate the nature of amygdala value-computing functions and how these functions work in collaboration with those of the PFC.

The RL literature suggests that state values can be computed in one of two ways: using a simple model-free algorithm or using a more sophisticated model-based algorithm (Daw et al., 2005; Dolan & Dayan, 2013; Sutton & Barto, 1998). Model-free RL algorithms compute the predicted value of a state (i.e., a stimulus or broader situation) by storing a running average of rewards obtained in that state on prior occassions. Because model-free algorithms rely on trial-and-error training to learn the value of individual states, they are inflexible and slow to adapt to changes in the environment.

In contrast, model-based RL algorithms compute the predicted value of a state based on an internal model of the structure of the world (i.e., knowledge of how different stimuli, situations, actions, and outcomes are linked together). The use of this knowledge allows the model-based algorithm to simulate what might happen in the future and to compute the predicted value of a state "on-the-fly" based on an integrative assessment of the immediate and future consequences of choosing to puruse that state. Thus, model-based algorithms are forward looking and flexible in that they rapidly update value predictions whenever any part of the overall model of the world is adjusted in response to new information.

An early and highly influential model proposed that subcortical regions such as the dorsolateral striatum and dopamine neurons support model-free computations, while the PFC supports model-based computations (Daw et al., 2005).[1] Given that prior work has been largely agnostic about the algorithmic basis of amygdala value signals, it has been unclear where the amygdala fits into the story. Based on existing evidence, we propose that the amygdala plays a central role in model-based value computations.

The studies that we reviewed above provide preliminary support for this idea given that they found amygdala activity to reflect both immediate and future consequences of decisions. More direct and compelling evidence comes from a study that explicitly compared amygdala value signals during a reversal-learning task with the value predictions generated by model-free and model-based algorithms (Prévost et al., 2013). In this study, human participants could use model-based knowledge about the task structure to anticipate when there would be a change in the value of one of the choice options and could use this information to guide their decisions.

Participants' reaction times indicated that they were indeed using model-based computations to guide their decisions. Critically, amygdala activity reflected the anticipated changes in value and this activity was significantly better accounted for by the value predictions of the model-based algorithm than the model-free algorithm (Prévost et al., 2013; for complementary findings in nonhuman primates, see Saez et al., 2015).

Another study (Klein-Flügge et al., 2019) had human participants perform a multistep decision-making task that required them to form a cognitive map of the task structure in order to earn rewards. Consistent with a model-based RL system, activity spanning the amygdala and hippocampus looked just like activity in the medial PFC and reflected knowledge of the higher-order structure of the task (i.e., how different position on the map were linked together and related to the task goal; Klein-Flügge et al., 2019). While it is unclear from this study where in the brain representations of task structure were initially constructed, the fact that these complex representations can be found in amygdala activity indicates that the amygdala has the information needed to compute forward looking and flexible value signals. In fact, amygdala activity did not correlate with a simpler form of reinforcement-based associative learning during this task (Klein-Flügge et al., 2019), further supporting the idea that amygdala activity is better explained by model-based RL.

Many other studies have examined amygdala functions using devaluation tasks. Although scholars have generally not framed these tasks as measuring sophisticated model-based value computations, they in fact do (see discussions in Daw et al., 2005; Dolan & Dayan, 2013). Thus, a variety of evidence favoring a model-based account of amygdala functions has existed, but has not been put together into a coherent narrative. In a typical devaluation task used with humans, monkeys, or rodents, a previously rewarded choice is devalued by feeding the individual the specific reward outcome until satiated (or by pairing it with a toxin in some versions of the task using nonhuman animals). The individual is then offered a choice between the devalued option and a new option. If the individual is swayed more by previous reinforcement (model-free computation), then they will choose the previously rewarded choice, even though it is currently worthless. However, if the individual uses their current state (being full) to look forward in time and realize that the previously rewarded choice will now lead to no reward (model-based computation), they will choose the new option (see Daw et al., 2005; Dolan & Dayan, 2013). While healthy individuals favor the new option, monkeys and rodents with amygdala lesions continue to choose the devalued option, indicating that the amygdala is needed for model-based value computations in this task (e.g., Hatfield et al., 1996; Izquierdo & Murray, 2007; Johnson et al., 2009; Málková et al., 1997). In line with these nonhuman animal findings, amygdala activity in humans correlates with the changing value of an outcome during a devaluation task (Gottfried et al., 2003).

Finally, it is worth noting that the amygdala is densely interconnected with regions that have been associated with constructing models of the world, including the hippocampus and medial PFC (Behrens et al., 2018; Gilboa & Marlatte, 2017; van Kesteren et al., 2012). It is difficult to imagine that the amygdala's value computations would not take this information into account.

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[1] Notably, the evidence accumulated since the publication of this model has not been clear-cut. There is little evidence that any brain region supports purely model-free computations (e.g., see discussion in Doll et al., 2012).

To summarize, there is growing evidence that the amygdala contributes to sophisticated model-based value computations. However, this idea has yet to be incorporated into prevalent models of value-based decision-making. We hope that the framework presented here will highlight the sophistication of the amygdala's model-based value computations and lead to new insights about how this region collaborates with the PFC in service of intelligent decision-making.

The Prefrontal Cortex and Action Planning

If the amygdala can support model-based value computations that flexibly contribute to the selection of goals, what then is the role of the PFC? Based on the extensive anatomical connectivity between PFC subregions and the motor system (e.g., premotor and primary motor cortices and motor neurons of the spinal cord; Passingham & Wise, 2012; Picard & Strick, 1996; Vogt, 2009; Yeterian et al., 2012), we suggest that the PFC is also involved in model-based computations, but in service of simulating and evaluating possible action plans to achieve those goals. Thus, while the amygdala and PFC are both involved in model-based RL, we suggest a division of labor that places the role of the amygdala closer to the ultimate motivations that give value to possible goal options, and places the PFC closer to the cognitive and action-related processes that organize and implement the means of achieving those goals.

Given that prior reviews have provided in-depth analyses of PFC functions, here we will present only a selective review of findings that highlight the role of the PFC in planning and evaluating actions. Although detailed coverage of the distinct functions of different PFC

subregions (Dixon, Thiruchselvam, et al., 2017; Passingham & Wise, 2012; Petrides et al., 2012) is beyond the scope of this article, we will make reference to several PFC subregions where relevant (Figure 2).

Model-Based Simulations of Possible Action Plans

In natural contexts, goal achievement often requires a series of actions performed over time in the correct sequence. Moreover, it is often the case that there are different action options to choose from, thus requiring a consideration of their relative utility—that is, their likely effectiveness and possible costs (e.g., a hungry individual might compare the utility of making a trip to the grocery store, unpacking food, and then cooking a meal, with the utility of making a reservation at a restaurant, driving to the restaurant, and then simply ordering food). Thus, it is critical to use model-based knowledge to mentally simulate possible action plans and to estimate their relative costs and benefits (Daw et al., 2005). This mental simulation may help individuals select an optimal action plan before committing to the implementation of specific actions, thereby reducing the chances of negative outcomes. A variety of evidence suggests that the PFC supports this type of model-based action planning.

A number of studies with humans and nonhuman animals have shown that PFC activity is sensitive to the model-based structure of tasks and have demonstrated that PFC lesions or disruption interferes with model-based action selection (Gläscher et al., 2010; Holroyd & Verguts, 2021; Hampton et al., 2006; Jones et al., 2012; Smittenaar et al., 2013). How exactly does the PFC make use of model-based knowledge?

Figure 2
A Depiction of PFC Subregions Mentioned in this Article
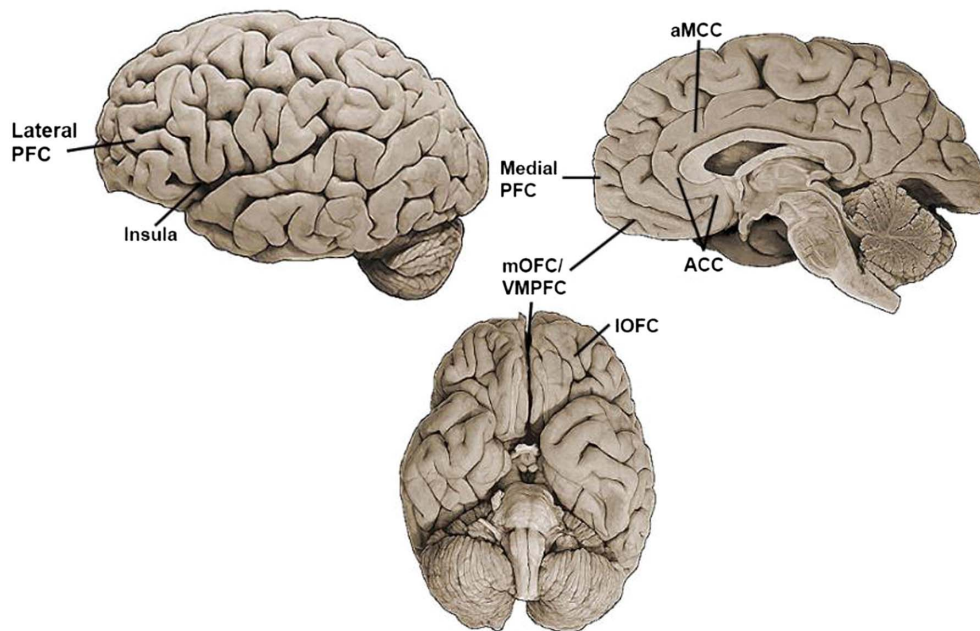
Note. We suggest that together, these subregions contribute to several key processes related to the simulation, evaluation, and implementation of action plans in service of achieving goals. ACC = anterior cingulate cortex; aMCC = anterior midcingulate cortex; lOFC = lateral orbitofrontal cortex; mOFC/VMPFC = medial orbitofrontal cortex/ventromedial prefrontal cortex; PFC = prefrontal cortex. See the online article for the color version of this figure.

The cognitive control literature suggests that the PFC may use models of task structure to flexibly plan and implement forthcoming actions in order to achieve a goal (Badre, 2008; Duncan, 2013; Koechlin & Summerfield, 2007; Miller & Cohen, 2001). For instance, fMRI studies with humans have shown that lateral and medial PFC activity increases when participants are asked to mentally simulate a sequence of actions (e.g., between 3 and 7 actions) that would be required to achieve a specific task goal or personal goal (Gerlach et al., 2014; Spreng et al., 2010; Zangemeister et al., 2016). In the previously mentioned study on economic savings decisions, lateral and medial PFC activity did not reflect the savings goal value, but did encode the length of the planned sequence of actions necessary to attain that goal, prior to the execution of the actions (Zangemeister et al., 2016). In line with this, single-unit recordings in nonhuman primates suggest that the lateral PFC is involved in transforming information about one's current goal into relevant action plans (Cai & Padoa-Schioppa, 2014). The ability to simulate temporally extended action plans may rely on the PFC's working memory capacities (D'Esposito & Postle, 2015).

Additionally, both fMRI studies with humans and single-unit recordings in nonhuman primates have demonstrated that PFC regions encode specific "if-then" rules that specify which actions are appropriate in different contexts (Bunge et al., 2003; Buschman et al., 2012; Wallis et al., 2001; Waskom et al., 2017). This rule encoding may underly the ability to construct flexible action plans as opposed to fixed action sequences that may be insensitive to context. Moreover, rules can enable sets of actions to be combined into meaningful groups and organized hierarchically with concrete actions nested under more abstract actions (e.g., specific, concrete actions involved in eating food may be nested under a more abstract rule or schema that specifies sets of interrelated actions involved in dining at a restaurant). In fact, a variety of evidence suggests that lateral PFC organization reflects an action control hierarchy, whereby more anterior parts of the lateral PFC support more abstract and temporally extended action planning functions, while more posterior parts of the lateral PFC support more concrete and immediate action planning functions (e.g., Badre, 2008; Badre & Nee, 2018; Christoff et al., 2003; Dixon, Girn, & Christoff, 2017; Koechlin & Summerfield, 2007; see also Holroyd & Verguts, 2021 for evidence that the ACC additionally contributes to hierarchical model-based action planning).

Finally, lesion studies have provided converging evidence that the PFC plays a central role in organizing action plans. Nonhuman primates with lateral PFC damage have difficulty performing tasks that require the sequencing of information in working memory (Genovesio et al., 2014; Petrides, 2000) and humans with PFC damage have difficulty planning sequences of actions and exhibit disorganized behavior (Szczepanski & Knight, 2014).

To summarize, a variety of findings support the notion that a cardinal function of the PFC is the ability to use task structure (model-based knowledge) to organize action plans, especially when multiple actions must be linked together in a sequence (Carlén, 2017; Duncan, 2013; Fuster, 2001). Importantly, these action simulations need not be composed of concrete movements such as driving to the grocery story. They can also include simulations of "cognitive actions" such as the cognitive steps involved in performing a task, or the cognitive strategy that could be used to regulate one's emotions (Gross, 2015).

Computing the Utility of Simulated Actions

During the process of simulating possible action plans related to a candidate goal, there may be different options that come to mind. These different action plan options must then be evaluated and compared in terms of utility to discern the specific course of action that may be optimal to reach a goal. Simply put, the brain needs to compute the following: How difficult are the candidate actions and how much time and energy will they require? Are any other costs involved? If effectively executed, are these actions likely to succeed in reaching the goal? Several PFC subregions including the medial PFC, aMCC, and anterior insula appear to play a key role in these action utility (cost vs. benefit) computations (Alexander & Brown, 2011; Holroyd & Verguts, 2021; Kouneiher et al., 2009; Rushworth et al., 2007; Shackman et al., 2011; Ullsperger et al., 2010).

Numerous fMRI studies with humans and single-unit recordings in primates have shown that these PFC regions encode specific action–outcome contingencies—that is, the likelihood that action X versus action Y will produce a favorable or unfavorable outcome given one's current goals (Brown & Braver, 2005; Hayden & Platt, 2010; Matsumoto et al., 2003; Procyk et al., 2016; Shima & Tanji, 1998; Ullsperger et al., 2010; Vogt, 2009). Correspondingly, lesions to these regions in nonhuman primates (especially the aMCC) impair the individual's ability to determine which specific actions to select (e.g., they may begin to perseverate on previously successful but no longer useful actions instead of switching to a new action; Rushworth et al., 2007; Shima & Tanji, 1998).

Beyond determining the likely success of candidate actions, it is also important to consider the amount of effort that will be required to reach a goal. PFC regions including the aMCC and anterior insula have been consistently linked to the representation of the effort involved in taking various actions (Chong et al., 2017; Croxson et al., 2009; Kennerley et al., 2009; Kurniawan et al., 2013; Prévost et al., 2010; Shenhav et al., 2013; Westbrook & Braver, 2016). Empirical evidence and theoretical models suggest that activity in these regions reflects the expected benefits of actions minus the effort cost (though as noted earlier, effort is not always a cost). One possibility is that these effort computations depend on predictions about interoceptive signals that are tied to the demands of executing particular actions (Barrett & Simmons, 2015; Craig, 2002; Touroutoglou et al., 2020). In any case, these regions play a critical role in evaluating the effort that would need to be invested if specific actions were to be taken.

To summarize, PFC regions including the medial PFC, aMCC, and anterior insula play a key role in evaluating the utility of action plans. In some cases, the utility-related signals in these regions have been interpreted more generally as common currency signals related to the desirability of goal options. However, there are several reasons to believe that these regions are specifically involved in evaluating actions. First, the aMCC and insula contain a somatotopic organization (i.e., separate zones representing different body parts) which would be useful for evaluating actions (Dum & Strick, 1991; Jezzini et al., 2012; Procyk et al., 2016; Vogt, 2009). Second, these regions exhibit robust activation during action planning and execution periods (Dixon et al., 2014; Vogt, 2009; Zangemeister et al., 2016). Finally, electrical stimulation of these regions has the effect of triggering action programs (Jezzini et al., 2012; Vogt, 2016). Thus, we suggest that coordination between PFC subregions may support action utility computations that specify the relative benefits versus

costs of possible action plans. This information may then be available to influence amygdala computations related to goal values.

PFC Regions May Be Involved in Aspects of Goal-Value Computations

Ventral PFC regions including the OFC/ventromedial PFC and ACC have long been implicated in value-based decision-making (Bechara et al., 1997; Damasio, 1994; Morrison & Salzman, 2011; Rolls, 2000; Wallis, 2007). However, their roles have been hotly debated (Zhou, Gardner, & Schoenbaum, 2021). As noted in the Introduction, some researchers have argued that these ventral PFC regions are involved in computing and updating goal values (Ballesta et al., 2020; Behrens et al., 2008; Juechems et al., 2019; Levy & Glimcher, 2012; O'Doherty, 2011; Padoa-Schioppa & Conen, 2017; Rich & Wallis, 2016; Rustichini & Padoa-Schioppa, 2015; Strait et al., 2014; Yamada et al., 2018). However, abundant data indicate that these regions are also engaged during memory tasks that have no value computation component at all (Addis et al., 2009; Andrews-Hanna et al., 2014; Gilboa & Marlatte, 2017; Hassabis & Maguire, 2009; van Kesteren et al., 2012). This suggests that ventral PFC regions may play a more general role in constructing rich and coherent knowledge structures (often referred to models of the world or schemas) that can be used to interpret current events and forecast possible future events in service of decision-making (Jones et al., 2012; Niv, 2019; Wilson et al., 2014; Zhou, Jia, et al., 2021). This model construction and future event forecasting function would facilitate value computations occurring in other regions (e.g., amygdala). More theory-driven studies will be necessary to disentangle these ideas.

Thus, although we have emphasized a general distinction between amygdala-mediated goal-value computations and PFC-mediated action planning computations, there may possibly be some ventral PFC regions that participate in the process of computing and updating values alongside the amygdala. Even if this is the case, it does not take away from the key message of this article, which is that the function of the amygdala in value computation is more sophisticated than previously appreciated.

Summary of the PFC's Contributions to Action Planning

We have reviewed evidence consistent with the notion that the PFC plays a role in simulating and evaluating possible action plans. Thus, while the amygdala may use a model of the world to compute the current value of particular events and specify goals, the PFC may use a model of the world to simulate and evaluate sequences of actions that may serve to achieve those goals. Importantly, our framework does not downplay the sophistication of the PFC's role in decision-making, but it does shift the emphasis from being a "master integrator and decider" to a sophisticated action planner. We suggest that input from the amygdala (and other regions) about broad need-relevant goal possibilities may in fact constrain the action plans generated by the PFC. In turn, these action simulations would influence the amygdala's value computations.

We note that PFC action plans may include the representation of specific "task goals" and other contextual information, but are informed by broader need-based goal values computed by the amygdala. Thus, we are not attempting to reassign to the amygdala

the well-documented representation of "task goals" in the PFC (Duncan, 2013; Miller & Cohen, 2001; Waskom et al., 2017). The key idea is that by representing specific task goals or objectives, the PFC provides the means by which these broader need-fulfilling goals (tagged with value by the amygdala) are realized.

Finally, it is informative to consider the implications of PFC expansion over the course of mammalian evolution, given its marked enlargement in great apes (Hill et al., 2010; Smaers et al., 2017; Wise, 2008). This expansion could potentially be interpreted in terms of the emergence of a regulatory function over subcortical regions. However, rather than a stage model of evolution in which cortical regions (including the PFC) were simply "stacked" on top of subcortical regions—as if serving as a new regulatory layer—evolutionary biology suggests a much more complex and dynamic interplay between cortical and subcortical evolution (e.g., Cesario et al., 2020). Moreover, the connectional architecture of the brain provides little evidence for a hierarchical organization in which the PFC serves as a "regulatory" structure with disproportionate influence on other regions (Parvizi, 2009; Pessoa, 2017).

Indeed, the evidence suggests that both the PFC and amygdala changed during evolution (e.g., with some parts of the amygdala increasing in size relative to other parts; Chareyron et al., 2011; Janak & Tye, 2015). Thus, the continued evolution of the amygdala may have enabled primates to generate more complex and temporally extended goals, while continued PFC expansion may have endowed primates with unprecedented ability to simulate extended sequences of cognitive and physical actions that could be useful in achieving those goals. When coupled together, these amygdala and PFC computations may enable primates to rapidly and flexibly specify and pursue goals with much less trial-and-error experience (Passingham & Wise, 2012).

Interactions Between the Amygdala and PFC

Interactions in Relation to Decision-Making

Consistent with our framework, many studies have reported evidence of cooperative interactions between the amygdala and PFC (e.g., Dal Monte et al., 2020; Gangopadhyay et al., 2021; Saddoris et al., 2005; Schoenbaum et al., 2003; Yizhar & Klavir, 2018; Zangemeister et al., 2016). For example, studies that have surgically disconnected the amygdala from the ventromedial prefrontal cortex/orbitofrontal cortex in nonhuman primates and rodents have demonstrated that interactions between these regions are necessary for value-based learning and decision-making, especially when goal values must be flexibly updated as contingencies change over time (Baxter et al., 2000; Gaffan et al., 1993; Gaffan & Murray, 1990; Murray & Rudebeck, 2018; Saddoris et al., 2005; Schoenbaum et al., 2003; Sharpe & Schoenbaum, 2016; Zeeb & Winstanley, 2013).

We propose that these interactions are critical for intelligent decision-making because they allow predicted goal values to be coupled with action plans (Figure 3). For example, imagine a student who is deciding between taking one class or another. One class might be more relevant to the student's major and will better position them for a summer internship, but will likely be difficult and require considerable effort. The other class might be easier and favor the student's grade point average (GPA). According to our framework, the model-based computations of the amygdala would contribute to value signals that specify the desirability of the two

classes based on how they will serve one's needs (e.g., the desire to gain competence by advancing one's knowledge in the major vs. the desire to demonstrate one's competence by earning a high GPA). In parallel, the model-based computations of the PFC would be involved in simulating possible action plans relevant to each course and their utility (i.e., the costs and probability of success of the actions that may be required by each class).

As information about the desirability of the classes is passed from the amygdala to the PFC, this would initially serve to focus the range of actions that may be considered by the PFC. In turn, the action utility computations of the PFC would be passed back to the amygdala and influence goal-value computations. This back and forth interaction would continue as new input is registered (e.g., related to needs or environmental affordances) and the front-running goal option may continuously shift. This might continue until amygdala–PFC interactions converge on one option being sufficiently more valuable than the other option, or until the individual is faced with a time limit and must commit to a decision.

Thus, our position differs from perspectives that implicitly or explicitly endorse the notion that the PFC functions as a master integrator and decider—that is, the idea that the PFC receives raw input from other regions and then serves as the master integration center that generates the values that drive decisions about both what to do (which goal to pursue) and how to do it (action planning). Instead, as we have noted, we envision constant interaction, with both regions playing complementary roles—amygdala computations being more informed by the ultimate motivations (current and future needs) that determine which goals are worth pursuing and PFC computations being more informed by action-related concerns (i.e., which actions are possible to execute and their relative benefits and costs). We suggest that action utility computations of the PFC do not directly lead to decisions. Instead, this information is passed back to the amygdala to shape goal-value computations, and as this information evolves in response to new inputs it is passed back to the

PFC, and so on, thereby creating a continuous cycle of interaction. Decisions then emerge from this collective activity (as well as the activity of other regions interacting with the amygdala and PFC).

Perhaps the strongest evidence for our framework comes from the previously mentioned study of economic savings behavior. Zangemeister et al. (2016) found that the amygdala but not the PFC encoded the value of the savings goal during the decision period, whereas the PFC (lateral PFC and aMCC) but not the amygdala encoded the planned action sequence to achieve the goal during the decision and action execution periods. Importantly, amygdala and PFC activity was functionally coupled during the decision-making period and was sensitive to the size of the anticipated reward outcome (Zangemeister et al., 2016), suggesting that their interactions may play a key role in the decision process. Although many other studies have shown that communication between the amygdala and PFC is critical for effective decision-making, they were not designed to test the specific division of labor we have proposed. We elaborate on this point in the Limitations and Future Directions section.

Interactions in Relation to Goal-Directed Behavior

While we are primarily concerned with intelligent decision-making, we provide a brief summary of how amygdala–PFC interactions may also contribute to effective goal pursuit once a decision has been made. During goal pursuit, we envision constant interaction between the amygdala and PFC as the individual monitors progress toward a goal and evaluates whether goal-value revisions or action strategy revisions are needed. The amygdala may contribute to the ability to persist toward goals by continuing to specify their value, which provides an overarching context that serves as the motivational fire to achieve a particular outcome.

The PFC may simultaneously contribute to the ability to persist toward goals by translating input from the amygdala into the sustained activation of a specific task goal and of relevant rules in

Figure 3
A Very Schematic Illustration of Amygdala–PFC Interactions
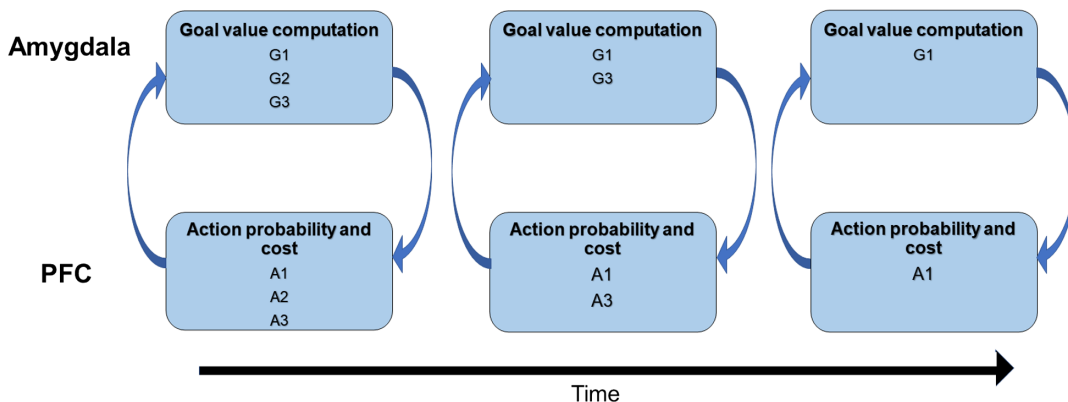
Note. In the simplest versions of our model, potential need-fulfilling goals (G1–G3) and potential actions (A1–A3) for realizing those goals are evaluated over time until one highly valued goal is converged on and pursued through a specific course of action. Here we illustrate a simple process of how goal options are evaluated and narrowed down. According to our framework, the amygdala tags possible goals with value based on current and future needs, while the PFC computes the probability of success and cost of possible actions. This information is sent back to the amygdala, which updates goal values, and so on. This process continues until a sufficiently valuable goal associated with a feasible course of action is identified and then pursued. PFC = prefrontal cortex. See the online article for the color version of this figure.

working memory. These representations held in working memory may guide attention to goal-relevant information (Barceló et al., 2000; Duncan, 2013; Everling et al., 2002; Kam et al., 2018, 2019; Rainer et al., 1998; Sakai et al., 2002) and specify when to emit or inhibit particular actions (Aron et al., 2014; Munakata et al., 2011). The PFC may also monitor the extent to which intended actions are effectively executed and producing expected changes in the world and may adapt action strategies on the fly when obstacles are encountered (Crone et al., 2006; Dosenbach et al., 2006; MacDonald et al., 2000; Miller & Cohen, 2001). Thus, goal-directed behavior may evolve as a result of parallel amygdala and PFC monitoring processes and the cooperative interactions between them.

This perspective differs in a key way from existing models of PFC–subcortical interactions, such as the model of working memory proposed by O'Reilly and Frank (2006). Consider the fact that using working memory to perform a cognitive task may be the action by which a broad need-fulfilling goal is realized (e.g., proving that you are smart and competent). The question then becomes, how does the PFC know which information to hold in working memory in order to move toward goal realization. In the O'Reilly and Frank (2006) model, the PFC slowly learns by trial-and-error which goal-relevant information to represent in working memory based on reward-prediction signals arising from the striatum. In turn, these striatum reward-prediction signals are updated based on prediction errors conveyed by midbrain dopamine neurons (which are themselves informed by associative learning in the amygdala). When this model is simulated, it leads to effective working memory task performance, but requires hundreds of trials to do so, far more trials than humans generally require.

In contrast, we suggest that the amygdala is playing a much more direct role in guiding what the PFC comes to represent. We also propose that the amygdala and PFC (and striatum and midbrain dopamine neurons) rely on a model of the world to perform their functions (Behrens et al., 2018; Doll et al., 2012; Prévost et al., 2013), rather than relying on a model-free (trial-and-error) approach, given that the latter cannot explain the speed and flexibility of human task performance. We propose that as long as the amygdala continues to specify that a broad goal has a high value, this information flows to the PFC and has the effect of constraining and stabilizing what the PFC comes to represent. (We suggest that, in some cases, the PFC may come to represent the "task goal" of effectively performing a working memory task based on the causal understanding that this may be a successful means of realizing the broader goal.) Indeed, one of the defining features of primates, and humans in particular, is the speed at which people can learn new tasks, often with very little feedback. This points to a model-based RL system.

While we have provided just a brief overview of how amygdala–PFC interactions may contribute to the performance of complex cognitive tasks, we hope that it may stimulate more attention to the role of the amygdala, which has often been ignored in favor of focusing on PFC–striatum interactions.

Although considerable evidence supports our proposal of complementary amygdala and PFC functions, we are quick to acknowledge that there are some limitations to the existing evidence, primarily due to the fact that many paradigms were not designed from a theoretical standpoint of trying to understand the complementary roles and inputs of the amygdala and PFC. Moreover, given their extended history of sharing information, we would expect to find some similarity in the information they represent, and some ability to compensate for one another if damage is present. Nevertheless, it is clear from existing evidence that abolishing amygdala input (via lesion or pharmacological inactivation) disrupts typical PFC function (Hampton et al., 2007; Rudebeck et al., 2017; Schoenbaum et al., 2003) and impairs decision-making (Bechara et al., 1999; Costa et al., 2016; Gaffan & Murray, 1990; Ghods-Sharifi et al., 2009; Winstanley et al., 2004), suggesting that the amygdala participates alongside the PFC in generating intelligent decisions. Our framework is intended to inspire new research that may clarify their respective roles with greater certainty.

The Relationship Between the Amygdala, Striatum, and Dopamine Neurons

How does amygdala function relate to broader motivational circuits? Considerable research has examined the value-related functions of dopamine cells in the midbrain (VTA/SN) and their relationship to the basal ganglia, particularly the striatum. We provide a brief overview of how these regions may perform complementary functions to the amygdala. Broadly speaking, midbrain dopamine-striatal connectivity patterns suggest a feed-forward organization that contributes to the translation of goal values, possibly from the amygdala, into motivated action (Haber & Knutson, 2010; Salamone & Correa, 2012).

Dorsal Striatum

The striatum is often divided into dorsal and ventral sectors. In contrast to the role of the amygdala in generating value signals that drive goal choice, the dorsal striatum (DS) appears to be more involved in computing action utility and driving action selection (Averbeck & Costa, 2017). This idea is supported by evidence of DS involvement in action sequence learning (Knowlton et al., 1996; Yin & Knowlton, 2006), representing action–outcome contingencies (Samejima et al., 2005; Seo et al., 2012), and influencing the speed and intensity of action execution (Jurado-Parras et al., 2020; Mazzoni et al., 2007; Panigrahi et al., 2015). For example, DS lesions lead to slower actions directed at goals due to increased sensitivity to movement effort costs, without affecting goal values per se (Jurado-Parras et al., 2020). Thus, the DS may work closely with action planning regions of the PFC (Haber & Knutson, 2010) and participate in the simulation and evaluation of possible actions to achieve goals, as well as invigorating specific movements during goal pursuit.

Ventral Striatum

Like the amygdala, the VS often shows anticipatory activity patterns that correlate with goal values (Bartra et al., 2013; Haber & Knutson, 2010). However, growing evidence suggests that the VS may inherit these goal-value signals from the amygdala and use them to stabilize choices over time (Averbeck & Costa, 2017; Kang et al., 2021). Reward-predictive activity in the amygdala precedes that in the VS and when the amygdala is damaged or inhibited via optogenetic stimulation it disrupts the contribution of the VS to goal-directed behavior (Ambroggi et al., 2008; Stuber et al., 2011).

Additionally, other work has shown that depletion of dopamine in the VS does not affect the hedonic quality of rewards, but does alter an individual's willingness to work to obtain rewards (Salamone & Correa, 2012; Westbrook & Braver, 2016). This suggests that the VS may be involved in action utility computations and may work closely with PFC regions that are also sensitive to action costs. Together, these striatal regions and the PFC may enable individuals to simulate extended action sequences and to expend the necessary effort to execute those actions in service of a goal (Westbrook & Braver, 2016). Thus, while the VS is often discussed in relation to valuation functions in general, it may be helpful to consider the functions of this region more specifically in terms of translating goal-value signals into motivated action output.

Dopamine Neurons

Midbrain (VTA/SN) dopamine neurons also play a key role in value-related processes. After a decision is made and an action is executed, individuals need to compare the actual outcome that is experienced to the predicted goal value and action utility in order to learn and update these predictions for subsequent decisions. Computational models and empirical findings suggest that midbrain (VTA/SN) dopamine neurons signal reward-prediction errors when outcomes are better or worse than expected (D'Ardenne et al., 2008; Gershman & Uchida, 2019; Glimcher, 2011; Kim et al., 2020; Schultz et al., 1997) and drive value updating in striatal and amygdala circuits (Nasser et al., 2017; O'Doherty et al., 2004; O'Reilly & Frank, 2006; Pessiglione et al., 2006). To compute reward-prediction errors, midbrain dopamine neurons may compare predicted goal values conveyed by regions including the amygdala with the actual outcomes that occur after action execution, conveyed by regions including the brainstem, hypothalamus, and PAG. In line with this proposal, prediction error signals have been consistently associated with the midbrain dopamine neurons and the striatum, but are less frequent in the amygdala, which tends to predominantly encode goal values (Averbeck & Costa, 2017; Belova et al., 2008; Paton et al., 2006). Although the prediction error function of dopamine neurons has often been cast in terms of model-free RL, it could just as well be interpreted in terms of signaling when to update models of the world (see e.g., Langdon et al., 2018).

To summarize, we have suggested that the amygdala is preferentially involved in predicting the value of possible future goal states, while the striatum and midbrain (VTA/SN) are preferentially involved in evaluating the utility of actions, and in updating action strategies when unexpected outcomes occur. However, these ideas are preliminary and require more studies that directly compare activity patterns across these regions.

Other Regions Involved in Decision-Making

Of course, there are regions that participate in decision-making other than those discussed here. We provide a brief overview of the roles of these regions in order to provide a broader context in which to understand the contributions of the amygdala and PFC.

In contrast to the flexible and domain-general roles of the amygdala and PFC, some regions appear to make domain-specific or species-specific contributions to decision-making. For instance, studies of perceptual decision-making suggest that regions including the posterior parietal cortex, frontal eye fields, and premotor cortex participate in early and late stages of the decision-making process (Churchland et al., 2008; Cisek & Kalaska, 2005; Ding & Gold, 2012; Shadlen & Newsome, 2001). Specifically, these regions accumulate evidence in ways that support the categorization of sensory stimuli (i.e., deciding what is being sensed in the environment) and contribute to relevant sensorimotor transformations that implement specific motor outputs (e.g., reaching or walking). Unlike the amygdala and PFC, however, these regions do not appear to be directly involved in domain-general value computations per se (e.g., Balan & Gottlieb, 2009).

Other regions such as the superior colliculus and PAG are involved in value computations, but in relation to solving very specific (possibly species-specific) problems. For example, these regions contribute to the implementation of prepared orienting and defensive behaviors (e.g., deciding to freeze or flee) in response to species-relevant cues when a rapid decision needs to be made (e.g., when an encounter with a predator is imminent; Bandler & Shipley, 1994; Cisek, 2019; DesJardin et al., 2013; Mobbs et al., 2007). These regions may also contribute to more flexible behaviors, but their functions appear to emerge from very specific and evolutionarily conserved value computations. In sum, while we have focused on the amygdala and PFC in this article, it is important to acknowledge that they operate in the context of other regions that also contribute to various aspects of decision-making.

Thoughts on the Development of the Brain's Decision-Making Circuitry

Most cultures have narratives about "stages of life" and about transitions that occur across the lifespan. The translation of these narratives into neurobiological theories (Casey et al., 2008; Shulman et al., 2016; Steinberg, 2008) often suggests that intelligent decision-making is slow to emerge over development and corresponds with the protracted maturation of the PFC-anchored cognitive control system and its ability to regulate the workings of the valuation system. Implicit (or explicit) in these theories are several assumptions: (a) the brain is composed of two distinct systems and poor decisions often reflect an imbalance between these systems; (b) the valuation system naturally has difficulty discerning what is good or bad for individuals and may often be unhelpful unless kept in check by a cool cognitive system; and (c) for this reason, the central nervous system may be somewhat "dysfunctional" until adulthood (but see Tottenham & Gabard-Durnam, 2017; Werchan & Amso, 2017). Recent theoretical and empirical work calls these assumptions into question and instead suggests that effective neurocognitive functioning reflects the development of a unified system for making decisions that are sensitive to the specific ecological niches and challenges faced at each point in development (Tottenham & Gabard-Durnam, 2017; Werchan & Amso, 2017).

There is good reason to believe that the amygdala (and valuation system more broadly) is intelligent even from early in life and that input from the amygdala provides the foundation for the proper functioning of the PFC (Tottenham & Gabard-Durnam, 2017). Childhood is a period when individuals must be keenly sensitive to cues that predict whether a person, place, or thing is harmful or a source of safety and pleasure. This enhanced sensitivity allows for the rapid formation of beliefs and predictions, as need-related goals are pursued, about how the world works and how needs get fulfilled or blocked (Dweck, 2017). As reviewed earlier, there is abundant

evidence to suggest that the amygdala plays a central role in learning about and guiding decisions based on goal values. Based on these considerations, Tottenham and Gabard-Durnam (2017) suggest that the precocious amygdala plays a key role in "teaching" the slower developing PFC about the world and what is important to the individual. Furthermore, amygdala lesions have a severe and persistent effect on socioemotional behavior that is more pronounced when the lesions occur early in development (Málková et al., 2010). Similarly, experiencing early-life adversity (e.g., low-quality caregiving) disrupts the typical development and functioning of the amygdala and has persistent effects on behavior and well-being (e.g., heightened anxiety) that are not remediated by PFC development (Cohen et al., 2013; Tottenham, 2012). Finally, studies have shown that the quality of early mother–infant bonding is associated with later amygdala structure (Moutsiana et al., 2015). Existing data thus suggest that effective learning about how to operate in the world is closely related to the amygdala valuation system and is compromised when individuals must adapt to highly stressful environments.

A second key point is that the PFC cognitive control system may be more functional early in life than is usually appreciated (Werchan & Amso, 2017). For example, evidence suggests that the PFC contributes to the use of behavior-guiding rules that support goal achievement at least as early as 3-years of age (Bunge & Zelazo, 2006). Therefore, a collaboration between the amygdala and PFC may begin early in life. As the amygdala forms increasingly complex need-fulfilling goals over the course of development, this may "push" the PFC to develop more sophisticated representations of rules and action plans in order to realize goals that can be conceived of but are currently out of our reach (see also Tottenham & Gabard-Durnam, 2017).

A key topic in the developmental literature is whether risky decision-making during adolescence is due to an imbalance between distinct brain systems, with the immature control system not yet having the capacity to regulate impulses arising from the brain's valuation system (Steinberg, 2008). We suggest that there may be alternative explanations and that existing accounts may, to some extent, reflect an adult value system—one that may not align with the adolescent value system (Yeager et al., 2018). Specifically, adolescents put a very high premium on their status among peers and, rather than being unable to control themselves, may be willing to risk physical harm to avoid humiliation or rejection from peers (Blakemore & Mills, 2014; Crone & Dahl, 2012; Somerville, 2013). Thus, we suggest that circuits including the amygdala give motivational priority to certain types of social goals during adolescence.

We further suggest that emerging executive function abilities of the PFC are often put to use in service of *these* goals. Adolescents sometimes demonstrate quite sophisticated control over their behavior—they strategize to form alliances, coordinate future activities, and engage in complex mentalizing and reasoning to understand, predict, and manipulate the behavior of others. Indeed, it has been argued that existing neuroimaging findings are incompatible with a simple PFC immaturity story (Crone & Dahl, 2012). Thus, it is unlikely that the root of adolescent patterns of behavior is that the amygdala (and valuation circuit more broadly) simply overpowers and essentially overrides the workings of the vulnerable PFC cognitive control system (see also Werchan & Amso, 2017). In line with this idea, a longitudinal study using a large sample of adolescents and young adults revealed that the amygdala and PFC exhibited positive functional connectivity across all ages, and

stronger functional connectivity was associated with less alcohol use (Peters et al., 2015, 2017). Although different interpretations are possible, one view is that this pattern may be opposite to the pattern (i.e., negative functional connectivity) that is generally predicted by the notion that the PFC and amygdala have an antagonistic relationship and that the PFC needs to "regulate" the amygdala. Instead adolescents appear more than capable of engaging PFC-mediated executive control functions, but may chiefly do so when they *are motivated* to (Crone & Dahl, 2012). Unhealthy (e.g., risky) behavior during adolescence may often have to do with how executive functions are used rather than immaturity of executive functions per se. While there is no denying that some PFC functions may continue to evolve into adulthood, there is little evidence to suggest that a clear shift between an immature PFC and mature PFC can be identified (Somerville, 2016).

To summarize, we suggest that the amygdala and PFC work together in age-appropriate ways at each point in development (Tottenham & Gabard-Durnam, 2017; Werchan & Amso, 2017). Yet, there is undoubtedly truth to the intuition that excessive emotion can "make" people act in ways that are not in their self-interest and that "calming down" can allow them to make better decisions. However, this may not be the result of the PFC regulating the amygdala. Instead, it may reflect a shift in the breadth of goals that are being considered in the amygdala–PFC circuit. In some cases, excessive emotion may reflect overprioritization of a specific goal at that moment within the amygdala–PFC circuit. Moreover, the desire to step back and calm down in order to have a more balanced assessment of different goals and make a "better" decision may itself be a value-guided process reflecting the emergence of new possible goals in the amygdala–PFC circuit. This means that rather than cool rational intellect alone reining in excessive emotions, it may actually be that a different type of valuation—one that is sensitive to immediate and future consequences—comes online and alters the initial goal valuations that generated the excessive emotion (Gross, 2015). Simply put, developmental changes in the ability to reflect on emotions and desired goal states and the capacity to regulate emotions may reflect more sophisticated goal-related processing and communication between the amygdala and PFC.

Implications of the Framework

In this section, we explore some of the implications of our proposed way of thinking about the amygdala and its relationship to the PFC.

Lesson 1: Expected Value Depends on Amygdala–PFC Communication

It is widely accepted that the expected value of a particular goal is a product of the goal's desirability/importance and some function of the probability of that goal being successfully realized (Eccles & Wigfield, 2002; Rangel et al., 2008). However, the way that expected goal value is generated in the brain remains unresolved. We have suggested that the answer to this question lies, at least in part, in the effective communication between the amygdala and PFC. While existing work has mainly searched for a relationship between the expected value and the activation strength of individual brain regions, we suggest instead that the expected value emerges

from the dynamic communication patterns (functional connectivity) between the amygdala and PFC.

Lesson 2: Motivation Is an Inherent Aspect of Intelligent Behavior

Different views of intelligence were popular in the early 20th century when intelligence became an object of scientific interest. David Wechsler, the creator of a popular IQ test, defined intelligence as: "the global capacity of a person to act purposefully, to think rationally, and to deal effectively with his [sic] environment." (Wechsler, 1944). In contrast, Lewis Terman, the creator of another IQ test (an adaptation of Alfred Binet's original assessment), defined intelligence as "the ability to carry on abstract thinking." (Terman, 1921). Wechsler's definition, but not Terman's, encompasses amygdala functions in that acting purposefully within one's environment arises from value-based decision-making.

Without minimizing the contribution of PFC functions to important outcomes in school and in life, those outcomes could not be attained if the individual placed little value on them or, said another way, had little or no motivation to achieve those outcomes. It would be difficult to identify highly successful individuals who had little interest in or saw little significance in what they were doing. Brilliant scientists like Einstein did not simply sit and exercise their PFC-mediated cognitive abilities for no particular reason. Instead, brilliant minds are noted for their dedication to what they study, and typically see its significance for understanding or improving the world. Our point is simply that PFC and amygdala functions always work synergistically to produce achievement, including intellectual achievement.

From a broader perspective, it is clear that functions linked to human intelligence, including abstract thinking, did not evolve in a vacuum for their own sake. They evolved in the context of key survival-related activities, including hunting in large coordinated groups, using tools in complex ways, and keeping track of myriad relationships and one's status within ever-growing social communities. To act purposefully and flourish within human society required a deeply ingrained synergy between evaluating possible goals and using various cognitive abilities in service of realizing those goals. Simply put, motivation may readily be seen as an *inherent* aspect of intelligence; motivation and intelligence are not two independent factors. We have already noted neuroscientific findings that support this idea. For example, Westbrook and Braver (2016) argue that working memory is inherently a motivated process because it carries a subjective effort cost that favors disengagement and requires a sufficient incentive to become initiated and remain engaged (see also Botvinick & Braver, 2015; Shenhav et al., 2013). In line with this motivational account of working memory, amygdala activation predicts the speed of responding in difficult three-back working memory tasks (with no accuracy trade-off) suggesting that it may play a role in supporting cognitive processes (Schaefer et al., 2006). Additionally, amygdala activation is associated with enhanced attention to, and memory encoding of, goal-relevant information (Anderson & Phelps, 2001; LaBar & Cabeza, 2006; McGaugh, 2004; Peck et al., 2013; Pessoa, 2010; Todd et al., 2012; Vuilleumier, 2005). Finally, Pessoa (2008, 2010) has argued that the value-based functions of the amygdala are so central to attention, memory, and decision-making that the amygdala cannot be considered a purely emotion region, but instead must be considered as a critical brain hub that contributes to a variety of complex cognitive abilities.

This conceptualization of intelligence and integrated brain function leads to a different perspective on why individuals may vary in success at school. We suggest that one important factor may be that some individuals are better able to internally generate interest and to perceive significance even in the decontextualized material often taught in schools. These individuals may more easily harness amygdala–PFC circuitry despite the often impersonal nature of the material. However, if provided with support for finding interest and significance in the material (or if provided with more personally relevant or interesting material), other individuals may learn and perform well too. Indeed, empirical work has demonstrated that when students are guided to think about how the classroom material (e.g., science lessons) is relevant and useful to their lives, it can lead to better learning (Hulleman et al., 2010; Hulleman & Harackiewicz, 2009). Thus, we suggest that optimal learning and performance depends on igniting amygdala–PFC interactions and there is much exciting research to be done in this area in the future.

Lesson 3: Reconceptualizing the Relationship Between the Amygdala and Psychopathology

Research has documented a link between amygdala activity and clinical disorders such as depression and anxiety (Etkin & Wager, 2007; Shackman et al., 2016; Whalen et al., 2002). Why does this link exist? It could be argued that over-activity in the amygdala generates excessive threat processing and negative affect and impairs normal functioning. However, this is unlikely to be the full account given the evidence reviewed earlier indicating that the amygdala is also involved in positive value computations. Furthermore, when amygdala activity occurs during unpleasant emotions this may reflect adaptive motivation to cope with negative life circumstances, rather than some sort of maladaptive response (Larsen et al., 2003). Finally, aberrant activity in the amygdala may be driven by faulty input from PFC regions (particularly the medial PFC and ACC) that contribute to negative self-beliefs and ruminative thought patterns (Berman et al., 2011; Dixon et al., 2020; Farb et al., 2011; Kross et al., 2009; Kucyi et al., 2014; Sheline et al., 2009). This activity, common in depression and anxiety (Gotlib & Joormann, 2010; Nolen-Hoeksema et al., 2008; Talmon et al., 2021) may in turn drive amygdala hyperactivity. These findings cast doubt on a modular perspective in which amygdala activity on its own is directly linked to psychopathology.

According to our framework, clinical disorders may often reflect a problem in the relationship between the amygdala and PFC, whereby goals are not matched with appropriate means for achieving them. In some cases, the individual may identify goals that they lack the means to realize, leading to frustration, negative self-beliefs, and discontent. In other cases, an individual may have the skills to realize goals, but have difficulty identifying adaptive goals that should be pursued. In simple terms, these cases may reflect either the PFC failing to identify effective strategies for realizing goals, or the amygdala failing to properly assign value to available goals, resulting in value being assigned to inappropriate/unhealthy goals or in little value being assigned to any goals, as in the anhedonia that often accompanies depression. Finally, as alluded to above, negative self-beliefs and ruminative strategies in the PFC may promote low expectancy for actions that could serve constructive goals or may

lead to poor amygdala-guided goal choices, which in turn may reinforce negative self-beliefs, creating a feedback loop in which neither appropriate goals nor means are selected.

A common theme across these examples is the notion that psychopathology may often reflect a broken or misguided partnership between the amygdala and PFC. Therefore, instead of framing psychopathology as a lack of PFC control over a wayward or overactive amygdala, we instead favor the view that the brain's natural state is one of harmony between the amygdala and PFC, and that a breakdown in this relationship can be a primary source of discontent.

Recent findings are broadly in line with this proposal (Gaffrey et al., 2021; Klein-Flügge et al., 2020, but see Gee et al., 2013). Klein-Flügge et al. (2020) found that higher satisfaction with life and lower experience of negative emotions in adults was associated with stronger functional connectivity between the amygdala and several PFC subregions (medial PFC, aMCC, ACC, lateral PFC, OFC). Similarly, Gaffrey et al. (2021) found that stronger functional connectivity between the amygdala and PFC (medial PFC and ACC) was associated with higher emotion regulation scores and lower negative affect in preschoolers. While these studies examined individual variation in healthy samples, the conclusions may well extend to clinical samples. Notably, these findings can be seen as opposite to what might be expected if the PFC was involved in reining in the amygdala, which might be weaker/negative functional connectivity. However, it should be noted that the nature of amygdala–PFC interactions may vary across different PFC subregions. Together, this work points to the relevance of investigating the relationship between amygdala–PFC communication patterns and psychopathology.

Limitations and Future Directions

Several possible limitations of our framework and several possible future directions are worth noting. First, direct evidence for our framework is currently limited by the fact that few existing studies were explicitly designed to test the nature of amygdala value computations (whether model-based or model-free), or tease apart amygdala and PFC contributions to decision-making based on the relative division of labor that we have proposed. We hope that this article will stimulate rigorous tests of our proposal via innovative task designs and new analytic methods. In particular, future studies could depart from the typical use of static stimuli and instead use experimental tasks that approximate more naturalistic situations (Paré & Quirk, 2017) involving rich task structure, dynamic stimuli, fluctuating needs, and freedom to select from a larger repertoire of actions. This would enable researchers to measure constantly evolving value signals (both goal value and action utility) and possibly make it easier to disentangle amygdala and PFC computations. Given the limited temporal resolution of fMRI, magnetoencephalography (MEG) or intracranial electroencephalogram (EEG) may be ideally suited for assessing the evolution of these decision-relevant variables in the human amygdala and PFC.

If a task presented sequential pieces of information that are relevant to computing the value of various goals, or of action strategies and expectancies, it could allow the experimenter to monitor the evolution of neural signals related to these components of decision-making. We would predict that value signals related to the formation of a goal (and online updates to those goals) would emerge earlier in the amygdala than PFC. Conversely, we would predict that signals reflecting action planning (and online updates to those plans) would emerge first in the PFC. While invasive recordings in nonhuman animals have the capacity to shed light on these timing-related questions, the evolutionary changes in the amygdala and PFC suggest that investigations in humans are necessary for a complete understanding of how we make decisions.

Second, the current framework would benefit from integration with data regarding specific amygdala nuclei, cell types, and microcircuit architecture (Duvarci & Pare, 2014; Janak & Tye, 2015; Pitkänen et al., 1997; Swanson & Petrovich, 1998). Recent advances in cell type- and projection-specific manipulations using targeted optical and molecular genetic methods have provided unprecedented insight into the microscale dynamics within the amygdala (Janak & Tye, 2015). For instance, these methods allow investigators to examine how specific cell groups respond to various stimuli and how stimulating or silencing a specific cell group in the amygdala affects other cell groups within the same nucleus, cell groups in another nucleus, or cell groups in another brain region (e.g., Ciocchi et al., 2010; Haubensak et al., 2010; Hong et al., 2014; Tye et al., 2011). Understanding these microcircuit interactions may ultimately help us to understand how information flows throughout different nuclei of the amygdala, what exactly is being integrated, and the full extent to which the amygdala is capable of sophisticated value computations. However, there are currently not enough data to bridge from this level of analysis to macroscale functions such as decision-making. Understanding how microcircuit dynamics contribute to decision-making computations will be a key task for future studies and may require new concepts and analytic methods, such as those used in network science to generate multiscale characterizations of complex systems (e.g., Bassett & Sporns, 2017).

Conclusion

In the framework proposed here, the amygdala and PFC play complementary roles in the process of co-constructing intelligent decisions. We have proposed that these regions are part of a coordinated model-based RL system in which the amygdala preferentially contributes to the computation of value signals related to potential goals that may serve the fundamental needs of the individual, while the PFC preferentially contributes to the mental simulation and evaluation of possible action plans that may achieve those goals. Just as important, we emphasize that intelligent behavior requires continuous interaction between these regions throughout the process of goal pursuit. We have also proposed that as individuals navigate a complex and evolving world they compute and recompute goal values via interactions between the amygdala and PFC.

This framework is a starting point that will need to be refined as further knowledge is gathered regarding the functional roles of different amygdala nuclei and PFC subregions and microcircuit details. In closing, we believe that the emerging picture of amygdala–PFC interactions has broad implications for scientists and how society in general views the mind. In some ways, depictions of the amygdala and PFC in the popular imagination have mirrored the age-old philosophical debate about the relative merits and status of reason (including self-regulation) versus passion. We note that in response to past philosophies that stressed the importance of reason prevailing over passion, David Hume (Hume, 1738) protested. Instead, he claimed that: "Reason is, and ought only to be

the slave of the passions, and can never pretend to any other office than to serve and obey them." The neuroscientific data suggest a more nuanced middle ground, in which passion and reason are not clearly separated in the brain. Both the amygdala and PFC support functions related to value, cognition, and self-regulation. We have proposed that the functions of these regions are complementary and contribute to the process of generating goals and of generating the means of pursuing them effectively.

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