Amygdala Tuning Toward Self and Other

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Human action is often proposed to be immoral at worst, amoral at best. According to such a worldview, people are inherently selfish and will act primarily to maximize their self-interested goals. Yet people have a surprising ability to forego their own self-interested desires to help others. For example, in economic games, people give far more than what would be expected from self-interest alone, and news reports provide many accounts of people putting themselves into risky situations for the benefit of others. What this suggests is that although people may be selfish, this selfishness is clearly bounded. In this chapter and project we examine how selfless goals can tune neural systems previously linked to self-preservation behavior. We highlight how the amygdala—once thought to be the seat of unconscious fear, threat, and negativity—may also be at the heart of compassion and other-focused motivation.

PROSOCIAL FEELINGS

Traditional Western thought has long conceptualized human nature to be selfish at its core. Philosophers and psychologists have contrasted reason against passion, or cognition against emotion, characterizing the former as an active, deliberate mode of behavior driven by rational considerations that inhibit animal drives and allow for appropriate social conduct, and the latter as an impulsive, reactionary mode that is driven by the world we encounter (Zelazo &

Cunningham, 2007). For example, in Plato's *Phaedrus*, the character Socrates describes the tripartite model of the soul, which separated reason or intellect from the "dark" appetitive passions (Plato, 1997). The Stoic philosophers extended this division by describing reason as a virtue, which one follows to become free from passion. Importantly, the Stoic philosophers characterized the passions as automatic and passive, and reason as an active, deliberative process that exerts control over the passions (Graver, 2009). To the extent that reason and the accompanying conscious control of passion is a virtue, iniquity and vice arise out of being overwhelmed by the automatic impulses that make up passion. Such impulses are described as drives and were originally directed toward objects relevant for self-preservation (White, 1979). Reflecting philosophical thought, early psychological theories similarly divided the human psyche and described interactions among its components (e.g., Freud, 1990).

Yet subsequent thought illustrated the importance of processes, once thought to be immoral, for moral behaviors. The philosopher David Hume argued that reason provided information about the means to an end, whereas passion provided the drives to engage in deliberated actions (Hume, 2000). The psychological literature too followed this shift in conceptualizing the interaction between the two putatively separate systems. For example, contemporary perspectives on moral judgments have shifted the emphasis away from rationalist approaches, where morality was regarded as a consequence of reasoning operations, and emphasized the role of moral emotions as direct inputs for such evaluations (Haidt, 2001). Moral emotions are distinct in that they inherently involve interpersonal features, and contrary to deliberative deductive processes, such emotions contribute to decision making through rapid and automatic appraisals of moral situations (Haidt, 2001). The neurologist Antonio Damsio posited the somatic marker hypothesis, which describes the way in which associations between emotional physiological states and encountered stimuli are processed in the ventral medial prefrontal cortex and, in conjunction with the amygdala, serve directing roles in decision making, particularly for complex or ambiguous situations (Damasio et al., 1996). In other words, emotions, or "passions," are useful in marking aspects of a situation and contribute to the information used in reasoning to navigate through the situation (Damasio, 1994).

This emerging perspective was echoed in subsequent work in the behavioral sciences. For example, many studies in the field of experimental economics have employed a "dictator game" paradigm as a way of examining the degree to which an individual benefits oneself over others. In this paradigm, a fund is given to a participant, which can be split and shared with another individual. However, the participant is also free to keep all of the endowment. Contrary to the decision that would maximize self-interest, the literature has

extensively documented that most people do not keep all the money, instead sharing some portion of it with the other individual (Hoffman, McCabe, & Smith, 1996). Demonstrations of fair behavior have held across manipulations of this experimental paradigm. For example, variants of the dictator game have been employed to demonstrate altruistic reciprocal behavior (Diekmann, 2004), where despite a decrease in fair behavior when the transparency of a participant's actions is reduced, people continue to share some portion of their fund rather than keep all of it for themselves (Dana, Weber, & Kuang, 2007). Other psychological research has demonstrated how situational changes influence selfish and selfless behavior. For example, recent work has shown that when people are placed under increased cognitive load, they demonstrate an increase in cooperative behavior (Rand, Greene, & Nowak, 2012). Using a variety of economic games, the authors demonstrated that individuals who make faster decisions contribute more money toward others, and experimental demands that force faster decisions promote similar cooperative behavior. Not only does such a finding challenge the view that automatic processes are directed toward only self-focused interests, but it also shows that rather than working completely in self-interest, people are able to demonstrate sensitivity toward others.

RETHINKING THE AMYGDALA

Although there are many systems involved in self- and other-focused processing, we restrict our focus to the amygdala for several reasons. Theory regarding amygdala function has mirrored the assumed division of the human psyche. Whereas the frontal cortices have been thought to be involved in reason and human virtue, the amygdala was thought to be related to our more "reptilian" brain—providing emotional signals that cloud human thought and are at the heart of anxiety, depression, and prejudice. Indeed, much of the early social neuroscience literature focused on how one could inhibit the amygdala during tasks for better emotional or self-regulatory outcomes. Furthermore, the amygdala has been traditionally thought to be at the heart of negative emotion specifically. In this project and chapter, we highlight that the amygdala does not simply function in the service of negative emotions, but it may also support positive emotions, reward processing, and prosocial behavior.

    Though the amygdala is often referred to as a unitary structure with designated functions, the view we put forward here instead aligns with research situating the distinct yet interconnected nuclei that comprise the structure within unique neural circuits that underlie different functional systems (LeDoux, 2004). The extended amygdala is comprised of several nuclei, each

with its own cellular (cytoarchitectonic) properties and connections to surrounding areas of the brain (e.g., Sah, Faber, De Armentia, & Power, 2003). These include the lateral, basal, and accessory basal nuclei, which make up the "basolateral amygdala," as well as the surrounding central, medial, and cortical nuclei (Davis & Whalen, 2001). From this perspective, the extended amygdala can support multiple specialized functions such as attention, reward reinforcement, and fear representation, depending on the amygdala subsystem (i.e., the particular pattern of neural populations within and across the subnuclei, and the larger networks to which they project). One approach to understanding how these nuclei interact and give rise to the multitude of functions associated with the extended amygdala is through the connection pathways between the structure and various subcortical and cortical regions of the brain. Output projections from subcortical regions, particularly the thalamus and hippocampus, carry sensory and stimulus-driven information to the basolateral amygdala, whereas pathways from cortical regions such as the prefrontal cortex modulate the amygdala via top-down processes. The amygdala serves as an informational, affect-driven hub between inferior temporal cortex regions involved in the perception and identification of salient stimuli and prefrontal regions involved in decision-making and executive functions.

From the basolateral amygdala, output pathways to various cortical and subcortical regions are associated with particular functions depending on the region to which they project. For example, the connectivity between the basolateral nucleus of the amygdala and the prefrontal cortex guides behavior based on valuation processes. The output of information to the orbitofrontal cortex (OFC) is important for decision-making processes and guiding goal-directed behavior (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Schoenbaum, Chiba, & Gallagher, 1998). Research has strongly supported the role of the OFC in decision-making and goal-directed behavior (Bechara, Damasio, Tranel, & Damasio, 1997), and lesions to this region especially impair social and moral behavior (Anderson et al., 1999). Cells in the OFC activate to information relayed from the basolateral amygdala in order to make choices and guide behavior (Schoenbaum et al., 1998). Along similar principles, outputs from the basolateral amygdala to the hippocampus influence other functions such as memory for emotional events and spatial learning (see Davis & Shi, 2000, for an overview). Indeed, which target area the amygdala activates is dependent upon the reinforcement signal of the information received by the basolateral amygdala, such as the nature of the sensory information from the thalamus (Davis & Whalen, 2001).

The importance of connectivity in supporting various functions is apparent in the contributions of the amygdala to reward circuits and appetitive behavior. Connections between the basolateral amygdala and striatal structures,

particularly the dopaminergic systems of the nucleus accumbens (NAcc) (McDonald, 1991), are relevant to reward learning in the context of conditioned reinforcement (Cador, Robbins, & Everitt, 1989; Davis & Whalen, 2001; Hatfield, Han, Conley, Gallagher, & Holland, 1996). Projections from the basolateral amygdala to the NAcc in the ventral striatum, and dopamine terminals in the adjacent ventral tegmental area (VTA), underlie two functional processes that give rise to approach (i.e., appetitive or reward-seeking) behavior (McDonald, 1991). Information from the amygdala about reward contingencies (e.g., associations between conditioned and unconditioned stimuli in a reward paradigm) is sent to the NAacc, where the dopaminergic system amplifies and outputs the signal (Davis & Whalen, 2001). Moreover, lesions of the basolateral amygdala have been found to reduce approach behavior (Cador et al., 1989). More broadly, the basolateral amygdala is critically involved in stimulus valuation, such as the representation of unconditioned stimuli via connectivity to the perirhinal cortex (Gewirtz & Davis, 1998). Studies supporting this role of the basolateral amygdala have employed unconditioned stimulus (US) devaluation paradigms, where a neutral stimulus is paired with an intrinsically rewarding unconditioned stimulus, and the unconditioned stimulus is subsequently paired with an intrinsically aversive stimulus (Davis & Whalen, 2001). Typical animals show reduced conditioned response to the neutral stimulus, but animals with lesions to the basolateral, but not the central, amygdala, block US devaluation (Hatfield et al., 1996). This pattern of lesions also blocks second-order conditioning in animals, which similarly relies on value representation (Everitt, Cador, & Robbins, 1989; Everitt, Morris, O'Brien, & Robbins, 1991).

Despite the documented place of the amygdala along neuronal circuits of reward and appetitive behavior, the amygdala has been regarded under prevailing theories as a structure involved in fear apprehension and aversion response (see LeDoux, 2000) through the provision of arousal cues that direct attention to the immediate environment. Earlier research restricted the amygdala's functional profile to negative affective states. For example, the amygdala, particularly the central nucleus (Davis & Whalen, 2001), has been heavily conceptualized as a crucial structure in an automatic system that detects threatening information in one's environment and directs subsequent behavior (Freese & Amaral, 2009). Research using functional magnetic resonance imaging (fMRI) in humans has shown that the amygdala is involved in the detection of threat and representation of negative affective states across multiple stimulus modalities, including the perception (Adolphs et al., 1999; Calder, Keane, Manes, Antoun, & Young, 2000; Morris et al., 1996) and evaluation (Adolphs & Tranel, 2004; Anderson, Spencer, Fullbright, & Phelps, 2000) of negative facial expressions, threat-related words (Isenberg et al., 1999), and aversive

odors (Zald & Pardo, 1997). This region is also known to play a critical role in the representation of fear, including the acquisition of fear responses through operant conditioning and the behavioral expression of the fear experiences (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; LeDoux 1998, 2000; Phelps et al., 2001). Given that this increased amygdala activation to fearful faces is not accompanied by subjective reports of fear (Morris et al., 1998), the functional role of the amygdala is specified to the processing of affective information rather than the entirety of emotional experience. The amygdala has been implicated in such functions by directing attention toward relevant information via projections from the central nucleus to the cholinergic systems of the basal forebrain (Everitt & Robbins, 1997; Holland & Gallagher, 1999).

The manner in which the amygdala utilizes such arousal cues to direct attention toward negative affective information has been further shown to be automatic, particularly in the context of perceptual attention (Anderson & Phelps, 2001). For example, when individuals were presented with fearful and happy faces for a perceptually subthreshold period masked by longer presentations of neutral faces, such that the individuals only had explicit experiences of apprehending the neutral faces and consequently did not show noticeable changes in their emotional arousal state, the amygdala demonstrated relatively greater signal intensity to masked fearful faces than to masked happy faces (Whalen, Shin, McInerney, & Rauch, 1998). Neurons in the central nucleus of the amygdala have been shown to change their firing rate as a function of tones that predict shock in a fear conditioning paradigm (Kapp, Silvestri, & Guarrci, 1996; Kapp, Silvestri, Guarraci, Moynihan, & Cain, 1997). It has been suggested that the automaticity of amygdala activation toward negative information could reflect habitual vigilance for negative stimuli through individual experience, or that it could reflect evolutionary and genetic forces that bias the automatic capture of attention (Cunningham, Raye, & Johnson, 2005).

Extending beyond the apprehension of negative stimuli alone, developments in attentional theories of the amygdala have further supported its role in processing various forms of meaningful information. Early neuroimaging studies examining the role of the amygdala in threat and fear processing documented greater activation of the region toward ambiguous stimuli, which requires further information before the engagement of approach or avoidance behavior (Whalen, 1998). For example, it was found that stimuli classified as being of high interest, which participants reported to be more difficult to interpret, elicited greater focal activation in the left amygdala (Hamann, Ely, Hoffman, & Kilts, 2002). The notion that the amygdala is sensitive to the uncertainty of stimulus contingencies may also account for the relative bias toward the amygdala representing negative information in the literature. It has been argued that fearful faces may have been found to be more effective in

activating the amygdala (Whalen et al., 1998) due to the ambiguity inherent in the lack of information about the source of a threat, rather than the specific emotional content itself (Davis & Whalen, 2001). The mechanism underlying this vigilant role of the amygdala was purported to be the amygdala-mediated lowering of neuronal thresholds in structures that comprise sensory systems such as the basal forebrain, via the modulation of acetylcholine. Similarly, the amygdala influences the activation of neurons with receptors particular to other neurotransmitters such as dopamine and serotonin, which then affects thalamic sensory processes (Whalen, 1998). The lowering of neuronal thresholds results in greater sensitivity to ambiguous stimuli and increases neural vigilance toward potentially important information.

More recent studies have shown that the amygdala is not only sensitive to fearful or negative stimuli but also to positive information. Again, this has been shown across various stimulus modalities, such as visual (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann et al., 2002; Liberzon, Phan, Decker, & Taylor, 2003) and verbal stimuli (Hamann & Mao, 2002). Thus, recent reviews demonstrate that amygdala activation is better characterized by a quadratic or U-shaped function, where the BOLD response is greater to both highly positive and highly negative stimuli, compared to neutrally valenced stimuli (Cunningham & Brosch, 2012; Cunningham & Kirkland, 2013; Cunningham et al., 2005; Mende-Siedlecki, Said, & Todorov, 2013). In fact, when the overall emotional intensity of the stimuli is controlled, there remains no relationship between positivity or negativity and amygdala activation (Anderson et al., 2003; Anderson & Sobel, 2003; Cunningham, Raye, & Johnson, 2004; Small et al., 2003; though see Anders, Eippert, Weiskopf, & Veit, 2008). This demonstrates that rather than sensitivity to specific valence, the amygdala is involved in processing stimuli of great affective intensity, that is, highly salient information.

This perspective of the amygdala as a brain region involved in processes that direct attention toward salient information, rather than soley tracking negative stimuli, is enforced by views that emphasize its role in integrating information from multiple sources. Though the implication of the amygdala in bottom-up processes has been described both here and extensively in the literature, there is also support for a role of the structure in top-down pathways: Amygdala response can be controlled through prefrontal processes (Ochsner & Gross, 2005). A recent magnetoencephalography study compared the fit of two models of amygdala function: a "dual" model that included both cortical and subcortical pathways to the amygdala, and a "cortical" model that excluded the subcortical pathways (Garrido, Barnes, Sahani, & Dolan, 2012). Data supported the dual model over the cortical model, demonstrating the importance of the subcortical pathway, particularly for early stimulus

processing and automatic appraisals of salient information. In fact, the position that the amygdala is specific only to negativity may be a consequence of regarding the amygdala only as a functional unit, rather than accounting for the numerous connections between its component nuclei and other regions of the brain. Our emphasis on distinguishing between the related functions of the amygdala based on its subsystems allows for the conceptualization of a flexible amygdala that tunes toward multiple types of relevant information and supports appropriate consequent processes.

As much as the amygdala demonstrates a general flexibility toward various forms of input information, there are still patterns of individual differences in the activity profile of the structure. For example, individuals with greater promotion focus, a motivational orientation characterized by relatively greater sensitivity to gains (Higgins, 1997), showed greater amygdala activation to positive stimuli, whereas individuals with greater prevention focus, a motivational orientation characterized by relatively greater sensitivity to preventing loss, showed greater amygdala activation to negative stimuli (Cunningham et al., 2005). Furthermore, the personality factors of extraversion and neuroticism are associated with increased amygdala responding to positive and negative information, respectively (Canli et al., 2001; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Cunningham et al., 2010). There are thus both general patterns of amygdala response as well as variations due to trait factors.

One way to account for both these features of amygdala activity is by conceptualizing the amygdala as a structure involved in the processing of motivationally relevant stimuli (e.g., Sander, Grafman, & Zalla, 2003). Following this initial relevance evaluation, additional resources are recruited to facilitate situation-appropriate responses (Brosch, Sander, Pourtois, & Scherer, 2008). This suggestion is based on appraisal theories of emotion (see Ellsworth & Scherer, 2003), which stand in contrast to the inflexible pattern-matching mechanism put forward by basic theories of emotion, and emphasize instead the importance of the subjective evaluation of a stimulus according to its importance for the individual. Thus, the amygdala functions as part of a larger affect system that informs us about what is important in the environment, and then facilitates the modulation of appropriate perceptual, attentional, autonomic, or conceptual processes in order to respond to present challenges or opportunities. On this view, differences in amygdala response between individuals and to various situations are not undefined noise, but rather the critical variation to be understood. Specifically, we expect that amygdala activation should vary as a function of the needs, goals, and values of the organism.

What is considered relevant can be defined by the usefulness of a stimulus for any momentary motivational structure of an individual. Because multiple goals can be important, the salience and priority of specific needs, goals,

and values shape responses. Therefore, motivational contingencies, and consequently the relevance of a given stimulus, may change continuously. For example, when one is hungry, food will be more relevant, whereas when one is in a dangerous neighborhood, potential criminals will be more relevant. Consistent with this idea, one study investigated neural mechanisms underlying attention toward food in participants both when hungry and satiated, thus varying the motivational relevance of the food stimuli within participants (Mohanty, Gitelman, Small, & Mesulam, 2008). When hungry, participants not only showed increased amygdala activation to pictures of food but also faster attentional orienting toward food cues and increased connectivity between limbic areas and parietal attention regions, compared to when participants were satiated. This point is also illustrated by the way in which more abstract social goals influence the apprehension of, and response to, encountered stimuli. A study that manipulated the processing goals of participants to evaluate only negative, only positive, or both positive and negative aspects of presented names found that amygdala activity was more strongly associated with the particular aspects of each name that signaled goal relevance (Cunningham, Van Bavel, & Johnsen, 2008), providing further support that the amygdala is engaged in processing aspects of stimuli that fit the current situational demands.

This pattern of results also suggests that previous research on social perception and prejudice may need to be updated. Specifically, studies using fMRI to study racial attitudes have suggested a role for the amygdala in the processing of threat associated with automatic prejudice (Cunningham et al., 2004; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Phelps et al., 2000). Yet, if the amygdala responds to motivationally relevant stimuli rather than threat per se, it may be possible to reverse these effects and find greater amygdala activity to in-group members, to the extent that these people are deemed motivationally relevant. Situations like this should not be unexpected: People who accurately identify, value, and cooperate with in-group members enjoy numerous functional benefits, including the fulfillment of their basic psychological needs (Allport, 1954). To test for this, in an fMRI study participants were randomly assigned to a mixed-race team, and brain regions involved in the processing of novel in-group and out-group members were examined (Van Bavel, Packer, & Cunningham, 2008). Though previous research on intergroup perception found amygdala activity, typically interpreted to reflect negative processing, in response to social out-groups, greater activity in the amygdala was found when participants viewed novel in-group faces compared to novel out-group faces.

This shift in our understanding of the role of the amygdala in social perception allows for important reinterpretations of previous amygdala findings. For

example, Wheeler and Fiske (2005) found that amygdala response to faces from Black and White social groups differed as a function of social goals. Under a social categorization goal, the amygdala was significantly more responsive to racial out-groups than in-groups. However, this pattern disappeared when participants had a goal to individuate each target or to visually inspect the targets' faces. Whereas out-group faces may have been deemed more relevant when social categories were being judged, in-group faces may have been deemed more important when a need to individuate was present. Thus, although these data were originally proposed to suggest that people could control their prejudiced responses, they may rather suggest that the relevance of the faces in the two conditions changed.

THE AMYGDALA AND PROSOCIAL BEHAVIOR

Given that humans are a highly social species, other people are highly relevant to most aspects of life. As such, it is important to process information about other individuals within and outside of one's group, as well as engage in the appropriate social behaviors. The social brain hypothesis posits that larger brain size and expanded volume in particular brain regions reflect the increased computational demands inherent to social organization in higher primates, including humans (Dunbar, 1998). Recently, evidence has been found for a link between amygdala volume and social network size and complexity in humans (Bickart et al., 2011). This relationship suggests that the amygdala may be part of a system that allows for the development of social relationships, community, and perhaps appropriate social behavior.

The amygdala is important for processing many forms of information that contribute toward more complex social judgments. Human faces are of particular significance for social evaluations, given the amount and relevance of information conveyed in facial expressions. Though the evaluation of human faces can rely on different dimensions (Todorov, Said, Engell, & Oosterhof, 2008), the trustworthiness of a face is one dimension important for most social outcomes (Oosterhof &Todorov, 2008). The critical role of the amygdala in supporting such evaluations of perceived trustworthiness in faces has been documented well, for both the untrustworthy (Engell, Haxby, & Todorov, 2007; Winston, Strange, O'Doherty, & Dolan, 2002) and trustworthy (Said, Baron, & Todorov, 2009; Todorov et al., 2008) poles of the dimension. Complimentary neuropsychology research has supported this role of the amygdala; for example, patients with bilateral amygdala lesions were found to have deficits in evaluations of trustworthiness based on facial features (Adolphs, Tranel, & Damasio, 1998). Together, the convergent evidence

demonstrates the importance of facial expressions for navigating complex social environments.

To maneuver within such complex environments moreover necessitates judging the intentions, decisions, and actions of other individuals, all of which are implicated in moral evaluations. Research has demonstrated that the formulation of moral judgments is an abstract social process also supported by multiple neural systems. Earlier fMRI studies have delineated the structures that support emotional processes broadly, including the extended amygdala and other subcortical nuclei, as well as those particularly necessary for moral emotions and evaluations, such as the superior temporal sulcus, medial frontal gyrus, and right medial orbitofrontal cortex (Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Moll, Oliveira-Souza, Eslinger, et al., 2002). Given the increase in functional connectivity between these regions for morally relevant stimuli, it is plausible that each of these structures supports different components, which together comprise the apprehension and evaluation of morally relevant information.

Although the evidence thus far implicates the amygdala in the processing of apprehended social and moral information, its contributory role in the expression of social behaviors has also been elucidated. Social behaviors vary in the degree to which the enacting agent, or other individuals, acquires gains, where prosocial behaviors consist of acts that confer benefits upon other individuals. One exceptional manifestation of prosocial behavior is altruism, which describes behaviors that extend assistance or confer advantages to others without anticipation of reward or at some cost to oneself (Piliavin & Charng, 1990). Altruism could be understood as a construct built upon component processes such as empathy and theory of mind; that is, to be altruistic requires empathetic ability. To the extent that empathy is involved in prosocial behavior then, the importance of the amygdala has also been shown (Decety & Jackson, 2004). Specifically, this role of the amygdala in empathetic and other prosocial behaviors is modulated by the neuropeptide oxytocin (Hurlemann et al., 2010). Oxytocin attenuates amygdala response to fear, resulting in a decrease in functional coupling between the amygdala and upper brainstem regions involved in autonomic responses to threat (Kirsch et al., 2005) by disrupting projections from the central nucleus (see Huber, Veinante, & Stoop, 2005). Decreases in fear processing and response may contribute to decreased distrust of others and, consequently, greater prosocial behavior (Labuschagne et al., 2010). Furthermore, given that empathetic behaviors necessitate adopting the perspective of another person and sharing their affective state (Decety & Jackson, 2006), there should be much overlap in the mechanisms supporting theory of mind and empathy. Indeed, greater amygdala activation has been found during performance on

tasks that require theory of mind processes (Baron-Cohen et al., 1999), and convergent neuropsychological evidence demonstrated impairment in performance on such tasks after amygdala damage (Adolphs, Baron-Cohen, & Tranel, 2002).

THE AMYGDALA AND THE GOALS OF SELF AND OTHER

Because goals shape amygdala activation (see Cunningham & Brosch, 2012, for a review), with the appropriate goal, the amygdala can become vigilant to the needs of others. To the extent that the amygdala is tuned to detect the needs of others, people will be able to more quickly detect those in need in a complex social environment and, as a result, be able to direct resources to these people. On this view, our "impulses" do not distract us from moral behavior, but rather can help guide us unconsciously to moral behavior.

To explore this hypothesis, we conducted a behavioral and fMRI experiment designed to systematically explore how positive self-focused and other-focused goals (i.e., helping oneself and helping others, respectively) shape amygdala function. In our study, participants were asked to identify people who would either (a) be most useful to help them with a goal (self-focused condition) or (b) be most in need of help from them given a particular context (other-focused condition). Given the adaptability of amygdala function in accordance with contextual demands, we predicted that with the appropriate goal, the amygdala would be sensitive to the needs of others. Consequently, we hypothesized that people should be able to more quickly detect individuals in need within a complex social environment and, as a result, be able to direct resources to these people.

Preliminary results from our study support this hypothesis. Specifically, although we found that the amygdala responded to the most trustworthy and untrustworthy faces regardless of whether participants were attending to themselves or others, we found that trait levels of empathy moderated the magnitude of this U-shaped function. Specifically, for participants lower in trait empathy, we found an altered U-shaped function with relatively greater activation for the self-focus than the other-focus condition. This effect is consistent with the idea that people are more sensitive to trustworthiness when they are seeking information that can be used to further their own goals. Importantly, this effect was reversed for participants who were higher in trait empathy. For these participants, activation was relatively greater when making other-focused judgments. In other words, high empathy appears to not only modulate amygdala response towards others, but more empathetic people

may also be more sensitive to information about trustworthiness when making decisions to help others.

Perhaps paradoxically, shifting focus away from the self and helping others may be among the most reliable paths to personal well-being and flourishing. For instance, a broad and representative longitudinal survey found that engagement in volunteer work enhances happiness, life satisfaction, self-esteem, sense of control over one's life, and physical and mental health (Thoits & Hewitt, 2001). Studies comparing elderly volunteers to nonvolunteers reveal that those who engage in volunteer work report greater life satisfaction, a stronger will to live, increased self-respect, and fewer psychological symptoms of depression and anxiety (Hunter & Linn, 1981), while experiencing lower mortality rates compared to nonvolunteers (Oman, Thoresen, & McMahon, 1999). More generally, a sizable corpus of research on altruism suggests a robust relationship between helping others and personal well-being (for reviews, see Post, 2005; Thoits & Hewitt, 2001). Thus, selfless acts undertaken at a cost to the self confer tremendous benefits upon the actor. In.additional analyses of this data set, we will examine the extent to which these effects, the ability to shift to the needs of others, may be associated with compassionate behavior and well-being.

CONCLUSION

This research project builds on the idea that our evolutionarily older brain systems are not solely a source of immorality and selfishness, but when tuned by our goals, can contribute to moral and just behavior. Thus, human flourishing does not come from the suppression of aspects of the self, but rather through the integration of all relevant processes together into a unified response. Specifically, theories of amygdala function suggest that it provides arousal cues to direct attention and facilitate effective responses to the environment. Previous conceptions of amygdala function restricted these responses to the self-focused objective of "avoiding personal harm." However, under our framework, the attentional benefits that the amygdala confers upon social perceivers can be leveraged to promote better prosocial decisions and, by extension, more effective prosocial actions. The amygdala is of critical importance to many of the social processes that make up the core of positive psychology, including empathy (Carr et al., 2003), attachment (Lemche et al., 2005), trust (Said et al., 2009), prosocial behavior (Cushing et al., 2008), and morality (Raine & Yang, 2006). In short, a detailed understanding of the amygdala's involvement in human social behavior holds great promise for elucidating the fundamental nature of positive psychology.

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