Six degrees of separation: the amygdala regulates social behavior and perception

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Recent human imaging work has expanded the view of amygdala function beyond early findings in animals, but two studies of an individual with bilateral amygdala damage now suggest that we should be thinking even more broadly.

Traditionally, the amygdala has gotten a lot of 'bad' press. Popular wisdom has portrayed the human amygdala as the center of an ancient animal id that drives us to rapid impulsive action before our more reasoned judgments can kick in. For a long time, it was considered to be a fear center or threat detector that is instrumental in allocating processing resources to potentially harmful events. This was in part because, thanks to research in nonhuman animals, the amygdala's role in fear learning was extremely well mapped. More recent studies in humans suggest that it is responsive to positive and arousing rather than to strictly negative events, as well as to ambiguous events[1,2]. In this issue, two case studies of an individual with bilateral amygdala damage indicate that ideas about amygdala function may need even further reconsideration. The connectivity of the amygdala places it at the center of the brain, a physical hub linking numerous distant regions, and it is positioned to allow emotions to influence how the rest of the brain works, from the first stages of stimulus encoding to regulating social behavior. Adolphs and colleagues examined these two functions and found that the amygdala may be important for regulating social distance[3] and influencing slower, explicit responses, as opposed to rapid automatic alerting to social signals of threat[4].

Although the amygdala has been studied in numerous ways, from molecular manipulations in mice all the way up to functional imaging in humans, patient SM's complete bilateral amygdala injury represents a unique opportunity to causally link the function of this well-studied structure to human behavior. Adolphs and colleagues took advantage of this opportunity to test both a previously unknown function of the amygdala and a well-established one. Kennedy *et al.*[3] studied the amygdala's role in regulating interpersonal distance. People automatically regulate the distance between themselves and others on the basis of feelings of personal comfort. Crowding unnecessarily close to a stranger in an uncrowded subway car or to a colleague at a meeting feels prohibitively uncomfortable and this reaction may serve as a powerful repulsive force in adjusting interpersonal distances (**Fig. 1**). In a series of elegant experiments, the authors demonstrate that SM fails to show evidence of these invisible social force fields that regulate close physical proximity, suggesting that the amygdala is crucial for the sense of interpersonal space.

In this study, SM was asked to face an experimenter at the interpersonal distance at which she felt most comfortable or to rate how comfortable she felt (ranging from perfectly comfortable to extremely uncomfortable) while standing at different distances from an experimenter. SM's preferred distance was consistently smaller than that of control subjects and she claimed to be comfortable even when standing nose to nose with the experimenter. This effect was robust in a number of variations of the procedure that controlled for alternate explanations of the main finding, including familiarity with the experimenter, the gender of the experimenter and the presence of eye contact during the experiment. Notably, SM reported that she was perfectly aware that other people had a sense of interpersonal space and she did not. She did not differ from the controls at the level of rational explanation; she simply did not feel the same discomfort with proximity that they did.

On the basis of their findings with SM, Kennedy *et al.*[3] predicted that the amygdala should be more active at close interpersonal distances in normal subjects. To test this prediction, they measured amygdala activation in control subjects using functional magnetic resonance imaging in response to reports that an experimenter was nearby or far away. As predicted, subjects showed greater amygdala activation at close distances. These data,

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Figure 1 A new study by Kennedy *et al.*[3] suggests that the human amygdala may be crucial for those feelings of discomfort with close physical proximity that help maintain appropriate social distances.

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together with SM's lack of aversion to close physical proximity, provide evidence that the amygdala is crucial for the sense of interpersonal space and may mediate emotional responses to personal space violation.

In addition to directly mediating the sense of discomfort, the importance of the amygdala in regulating social distance may also reflect emotional learning of social conventions. Parents socialize their children by using reward and punishment to teach them the emotional importance of social norms. Indeed, SM's disregard for interpersonal distance despite knowledge of the typical rules of social engagement parallels the established role of the amygdala in fear-conditioned responses, where autonomic responses are abolished, but factual knowledge of events that predict unpleasant events remains intact[5]. Moreover, there are different rules for social proximity for different relationships (parents or lovers versus strangers) and these vary across cultures. As these rules are culturally learned, amygdala responses to specific social stimuli in specific contexts may arise from developmental experience. Recent research has shown that the amygdala responds preferentially to different stimuli depending on their social context[6]. As the amygdala is an important hub in networks implicated in social learning[7], socialization may partly be a process of tuning amygdala responses during development.

Another potential account of the finding that SM has no instinctive discomfort at close social distances is that she lacks a rapid amygdala response that directs attention to socially and emotionally salient events. In support of this explanation, there is evidence that fearful faces, which are thought to signal danger in the environment, are processed more quickly than other facial expressions and activate the amygdala more than neutral faces, even when presented subliminally[8]. This evidence has often been interpreted in terms of an evolutionary advantage for responding to threatening events faster than the speed of thought. There is also conflicting evidence that awareness is required for the amygdala to respond to fearful faces[9]. A study of SM by Tsuchiya *et al.*[4] challenges the notion that the amygdala is responsible for rapid processing of fearful faces by showing that SM has a normal capacity for detecting fearful faces when they are presented rapidly or at the threshold of awareness.

SM was shown images flashed on a screen (for 40 ms), with a fearful face on one side and a neutral face on the other. Although she showed the same degree of speed and accuracy as controls, her intensity ratings of fearful expressions were much lower, suggesting that, for her, they lacked their intense fearful quality. Two additional experiments employing visual search and interocular suppression further supported the notion that SM demonstrated enhanced awareness of fearful facial expressions. From these results, Tsuchiya *et al.*[4] conclude that the amygdala is not necessary for rapid implicit detection of fearful facial expressions. Instead, they propose that it contributes to slower processes involved in explicit recognition of facial expression in particular and in social judgment in general.

Although Kennedy *et al.*[3] and Tsuchiya *et al.*[4] propose a seductively simple account of amygdala function, the results from these two case studies paint a complex picture of intact and spared capacities following amygdala damage. Although amygdala damage leaves explicit knowledge of interpersonal distance norms intact, it impairs the potentially implicit and automatic use of these norms in regulating behavior. Conversely, although amygdala damage impairs direct explicit knowledge about the fear quality of faces, it leaves their rapid and relatively automatic processing intact.

Whether the amygdala is necessary for the rapid perceptual processing of social and emotional salience in general, rather than for fear faces in particular, may still be an open question. First, the finding that SM has a normal ability to more rapidly detect fear faces may not generalize to more intense emotional stimuli. This may be because fearful faces in experimental contexts fail to elicit sufficient autonomic arousal[10], which has been shown to be a critical dimension in accounting for emotional salience. Indeed, amygdala lesions reduce autonomic arousal responses to subliminally presented emotionally arousing images[11]. Amygdala lesions also impair the enhanced awareness associated with arousing stimuli when attentional resources are limited, but leave intact the enhanced awareness associated with visually distinctive events[12]. These results fit with nonhuman animal studies demonstrating that amygdala stimulation results in altered cortical arousal[13].

Given that amygdala damage leaves enhanced awareness associated with visually distinctive events intact[12], the rapid detection of fear faces may be independent of the amygdala because the fear face advantage is related to low-level visual characteristics of fearful faces. Fear faces are characterized by the exaggerated whites of the eyes, and this information is extracted in the early stages of visual processing of faces[14]. Thus, more rapid detection of fearful faces may be a result of particularities of visual features: their visual rather than motivational salience. Tsuchiya *et al.*[4] go to substantial lengths to account for these potential contributions using face-morphing procedures that control the global physical distance between neutral and fear faces, but this process may not equate physical differences in the especially visually salient region around the eyes, particularly the whites of the eyes. As such, it remains possible that, although SM's difficulties in explicit fear recognition stem from a failure to use emotional information from the eyes[15], these features may still serve as a source of physical salience in the visual cortex that can be used in the absence of rapid amygdala modulatory influences on perceptual encoding[12]. Thus, it might be too early to discount the early modulation account.

It is important to answer whether social and emotional influences on stimulus encoding reflect predominantly early feedforward inputs from the amygdala or later re-entrant influences onto the amygdala from the cortex and back again. However, the studies appearing in this issue highlight the idea that the broader salience of social and emotional events, and the amygdala's role therein, is not confined to those first fleeting moments of stimulus encoding. Instead, it may extend to time scales across multiple orders of magnitude, from stimulus consolidation in the present moment to the differential consolidation of these moments into our neural and social networks. The old image of the amygdala as an automatic threat detector may come to be replaced with a picture of the amygdala as a hub of distributed networks that mediate rapid and extended responses to the emotional salience of people, objects and events. Furthermore, just as it is physically central in the brain, the amygdala may serve as a hub of social networks, influencing the literal degrees of separation between ourselves and the social world around us.

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