The role of the amygdala in visual awareness

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Pessoa and colleagues recently reported the novel finding that objective awareness of a negative stimulus is associated with coactivation of the amygdala and fusiform gyrus. Based on the neuroanatomical connections of the amygdala, we suggest that the amygdala is acting to increase neural activity in the fusiform gyrus, thereby increasing the likelihood that visual representations that have affective value reach awareness. The psychological consequence is that a person's momentary affective state might help to select the contents of conscious experience.

Introduction

There are well-documented projections between the amygdala and the ventral visual stream in primates [1]. Neuroimaging studies show that 'affective' objects (i.e. objects that are known to elicit an affective change, such as faces depicting emotion) increase activity in both the amygdala and ventral visual cortex [2]. The psychological consequences of these projections and the coactivation of the amygdala and ventral visual stream are the subject of intense research interest. We believe that a recent study by Pessoa and colleagues [3] enables novel speculation of the role of the amygdala in visual awareness, suggests provocative hypotheses regarding the relationship between affective states and sensory processing, and raises important questions about whether the distinction between affect and cognition is respected by the human brain.

The role of the amygdala in visual awareness

Emerging evidence suggests that amygdala activity is linked to the visual awareness of objects [4]. A recent fMRI study by Pessoa and colleagues [3] builds on these findings by demonstrating that amygdala activation is associated with the likelihood that visual representations that have affective value reach awareness. In this study, participants viewed backwardly masked presentations of faces that depicted fear, happiness or neutrality. Each target face was presented for 33 or 67 ms, after which participants indicated whether the face depicted fear or not. A signal detection analysis yielded an index of objective awareness for each presentation time (i.e. responding in a behaviorally correct way at a greater-than-chance level, even in the absence of conscious awareness). All participants showed amygdala–fusiform gyrus (FG) coactivation and objective awareness on 67 ms trials. In the 33 ms trials, only participants who had objective awareness of the faces depicting fear (N = 8) showed enhanced activity in the amygdala and FG; no such increase was observed among participants who did not show objective awareness of these faces (N = 19) (Figure 1). These findings demonstrate that activity in the amygdala and FG (a portion of the ventral visual stream where activity is associated with normal conscious awareness of stimuli [5]) is related to awareness of visual objects.

Pessoa *et al.* hypothesized that amygdala activity depends on visual awareness (for a discussion on the debate regarding whether amygdala activity is attention dependent, see Ref. [6]). However, neuroanatomical evidence suggests an alternative hypothesis: the amygdala enhances visual awareness. In primates, the basal nucleus of the amygdala projects to the entire ventral visual stream, from association cortex back to primary visual cortex; projections in the other direction are sparse [1]. Also, individuals who have amygdala lesions show decreased FG responses to affective objects compared with normal individuals [7], further supporting the idea that the amygdala enhances activity in the ventral visual stream and, correspondingly, visual awareness of affective objects. (The suggestion that amygdala activation is necessary for visual awareness does not imply that such activation always produces awareness.)

Implications for the role of affect in visual awareness

Our interpretation of the Pessoa *et al.* [3] study suggests several provocative implications for a science of the mind. First, the variability in people's conscious awareness of briefly presented affective objects (reported by Pessoa *et al.*) means that the environment might literally look different to different people. Previous studies using fast presentations of affective stimuli have relied on subjective estimates of visual awareness to demonstrate that the target objects of interest were not seen (e.g. asking participants whether they saw the targets after the scanning session). Using an objective measure of awareness, Pessoa and colleagues found that many participants are aware of faces that are presented for short durations, which implies that, in real life, these people might also see microexpressions of smiles and frowns (that are invisible to others). Such variability might instantiate individual differences in personality dimensions, typified by sensitivity to affective information (e.g. neuroticism and introversion) and might serve as a risk factor for developing clinical disorders, typified by an enhanced sensitivity to unpleasant stimuli or a lowered sensitivity to positive stimuli (e.g. anxiety and depression).

Second, what people literally see in the world around them might be partially determined by their basic (or core) affective state. The amygdala is an integral component of a distributed affective circuit in the mammalian brain that

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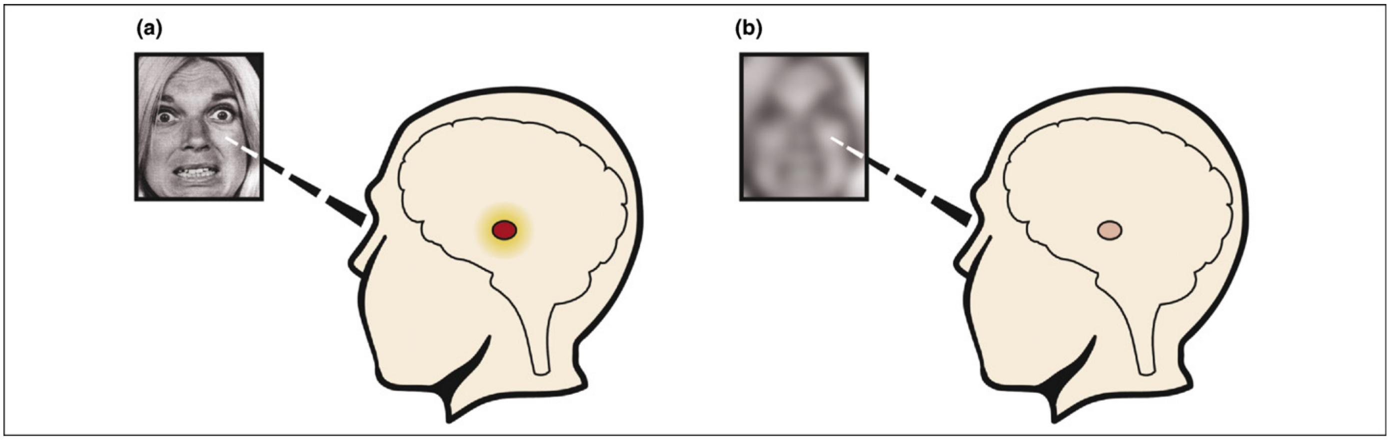

Figure 1. Visual awareness is associated with amygdala activation. In the Pessoa *et al.* study [3], participants viewed backwardly masked images of faces that depicted fear, presented for either 33 ms or 67 ms. All participants showed greater amygdala activation when viewing fearful faces that were presented for 67 ms, compared with faces that depicted neutral expressions. **(a)** Pessoa *et al.* found an increase in amygdala activation (as well as fusiform gyrus activation, which is not shown in the figure) only among those participants who showed objective awareness of 33 ms presentations of faces that depicted fear. **(b)** Participants who did not show objective awareness did not have significant increases in amygdala activation. Given the excitatory projections from the amygdala to the ventral visual stream, this finding suggests that the amygdala enhances visual awareness for objectives with affective value. [Note that low-frequency spatial information reaches the amygdala via the magnocellular visual pathways of the thalamus [15], suggesting possible amygdala activation in (b)].

computes a psychologically primitive state of pleasantness or unpleasantness (a 'core affective state' [8]). This circuit (which includes the ventral striatum, orbitofrontal cortex and ventromedial prefrontal cortex) instantiates a core affective state by integrating sensory information about a stimulus with a representation of how the stimulus affects the person's internal (somatovisceral) state [9,10]. A provocative implication of the Pessoa *et al.* findings is that core affective states not only influence how people interpret objects already seen but might determine what people visually detect in the first place. As a result, individuals in unpleasant affective states might be more likely to be visually aware of brief visual events (e.g. quick changes in facial muscle movements) or have an enhanced ability to detect objects that blend into their background (e.g. snakes in the grass). In some circumstances (e.g. where the base rate of the threat is low), such vigilance might pose a risk for mental illness. (Note that there is debate over the role of the amygdala in affective experience, and studies have shown that patients who have amygdala damage report the same levels of positive and negative affective experience as healthy controls [11]. However, these studies used retrospective reports of affective experience, which rely on beliefs about emotional experience and might not accurately reflect the actual experiences [12].)

The third, and perhaps broadest, implication of Pessoa *et al.* is that the cognition–affect distinction might not be respected in the brain. Traditionally, affect is thought to be cognitively impenetrable and implemented in subcortical regions of the brain, whereas cognitive processes that are implemented in prefrontal areas regulate affective processing after the fact (discussed in Ref. [4]). Therefore, it has been assumed that cognition and affect represent a neurobiological distinction. However, if parts of the brain that are involved in instantiating an affective state modulate sensory processing, then this distinction is called into question. Cognition has typically been defined as any process that modulates sensory processing [13]. If the amygdala, along with other areas that together compute core affective states, modulates activity in the ventral visual stream, then affect acts as a form of cognition.

Prospects for the future

Further research is needed to understand the ability of the amygdala to modulate sensory processing and awareness of objects in the physical world, but perhaps the real innovation of the findings from Pessoa *et al.* [3] lies in the provocative implication that it is possible for core affective circuitry to select the contents of consciousness. Neuroanatomical evidence indicates that the amygdala and other parts of core affective circuitry modulate the attentional matrix in the brain. Affective circuitry might enhance sensory processing (i.e. apply attention) by direct projections to sensory cortex (consistent with the Pessoa *et al.* study), but it might also modulate the attentional matrix through indirect projections to the dorsolateral prefrontal cortex (via the orbitofrontal cortex), thereby influencing goal-based attention. Core affective circuitry also projects to the basal forebrain, brainstem and thalamic nuclei, which are important sources of bottom-up forms of attention that have a role in unifying conscious experience [14]. Through these projections, brain regions that are involved in establishing a core affective state might have strong control over processing throughout the entire cortical mantle, influencing which contents are experienced in the moment and which are likely to be stored in long-term memory.

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Spatial cognition in apes and humans

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The debate on whether language influences cognition is sometimes seen as a simple dichotomy: cognitive development is governed either by innate predispositions or by influences of language and culture. In two recent papers on spatial cognition, Haun and colleagues break new ground in bringing together a comparative cognition approach with a cross-linguistic framework to arrive at a third position: that humans begin with the same spatial reference frames as our near relatives, the great apes, and diverge later owing to the influence of language and culture.

Introduction

In two recent papers [1,2], Haun and colleagues unite two important current lines of research: cross-linguistic studies of language and cognition [3], and studies in the comparative cognition of humans and great apes [4,5].

This research draws on a large-scale investigation of cross-linguistic differences in spatial semantics [6,7] that has identified three frames of reference that speakers use to identify the location of an object. The egocentric (or relative) frame describes the location of an object relative to the speaker, as in 'the chair on my left'. The object-centered (or intrinsic) frame describes locations relative to a landmark object, as in 'the chair in front of the fireplace'. Finally, the geocentric (or absolute) frame describes locations relative to a global frame, as in 'the chair in the northwest corner'. Languages can use more than one of these frames, but in many cases one frame is dominant. In particular, the egocentric frame is dominant in English, Dutch and German, whereas the geocentric frame is dominant in Tzeltal (southern Mexico) and Hai||om (Namibia), among others. Using a clever set of tasks, researchers have amassed evidence that people given nonlinguistic spatial tasks show a strong tendency to use whichever frame is dominant in their language [3,6] (but see Ref. [8]). This work has been a major impetus in reviving the Whorfian question of whether the language we speak influences the way we habitually think [9–11].

Evidence of linguistic effects on spatial cognition invites the question of how they develop. Do we begin life with natural proclivities or instead with 'blank slates' on which language, culture and other experience impose spatial frames? Haun *et al.* addressed this question in a bold and ingenious set of studies that combines cross-linguistic developmental comparisons with cross-species comparisons between humans and our close relatives, the great apes.

Spatial frame of reference

Haun *et al.* [1] compared Dutch and German speakers, whose language (like English) primarily uses an egocentric frame of reference, with speakers of Hai||om (a Khoisan language spoken in Namibia), which primarily uses a geocentric frame. They used a hide-and-search task with the five-object arrays shown in Figure 1. The subject (S) watched the experimenter hide Target 1 under one of the five identical objects on Table 1, then moved to Table 2 (now facing the opposite direction) and searched for Target 2. The location of Target 2 was determined by one of three rules, corresponding to the three spatial frames. For example, if Target 1 was in the northwest corner of Table 1 (and directly left of S) then, in the geocentric condition,

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