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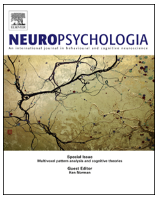

# The role of the amygdala and the basal ganglia in visual processing of central vs. peripheral emotional content

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## ABSTRACT

In human cognition, most relevant stimuli, such as faces, are processed in central vision. However, it is widely believed that recognition of relevant stimuli (e.g. threatening animal faces) at peripheral locations is also important due to their survival value. Moreover, task instructions have been shown to modulate brain regions involved in threat recognition (e.g. the amygdala). In this respect it is also controversial whether tasks requiring explicit focus on stimulus threat content vs. implicit processing differently engage primitive subcortical structures involved in emotional appraisal.

Here we have addressed the role of central vs. peripheral processing in the human amygdala using animal threatening vs. non-threatening face stimuli. First, a simple animal face recognition task with threatening and non-threatening animal faces, as well as non-face control stimuli, was employed in naïve subjects (implicit task). A subsequent task was then performed with the same stimulus categories (but different stimuli) in which subjects were told to explicitly detect threat signals.

We found lateralized amygdala responses both to the spatial location of stimuli and to the threatening content of faces depending on the task performed: the right amygdala showed increased responses to central compared to left presented stimuli specifically during the threat detection task, while the left amygdala was better prone to discriminate threatening faces from non-facial displays during the animal face recognition task. Additionally, the right amygdala responded to faces during the threat detection task but only when centrally presented. Moreover, we have found no evidence for superior responses of the amygdala to peripheral stimuli. Importantly, we have found that striatal regions activate differentially depending on peripheral vs. central processing of threatening faces. Accordingly, peripheral processing of these stimuli activated more strongly the putaminal region, while central processing engaged mainly the caudate nucleus.

We conclude that the human amygdala has a central bias for face stimuli, and that visual processing recruits different striatal regions, putaminal or caudate based, depending on the task and on whether peripheral or central visual processing is involved.

## 1. Introduction

Much of what we know regarding the functional anatomy of neural pathways connecting to the amygdala comes from auditory fear conditioning studies in the rat animal model (Whalen et al., 2009; LeDoux & Phelps, 2008). A large difference between rodents and primates can be recognized in the processing of social stimuli such as faces (Buchanan, Tranel, & Adolphs, 2009). In primate visual and affective processing, faces can be considered as a special class of objects (Critchley et al., 2000; Hershler, Golan, Bentin, & Hochstein, 2010; Johnson, 2005). Faces are preferentially processed in central vision, where they are screened for high-resolution foveal information (Kanwisher, 2001; Levy, Hasson, Avidan, Hendler, & Malach, 2001). Studies in humans suggest the existence of foveally-biased specialized regions along the occipito-temporal ventral visual pathway to extract meaning from faces: the occipital gyrus, the lateral occipital (LO), the superior temporal sulcus (STS), and regions in the fusiform gyrus, such as the fusiform face area (FFA) (Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997). Accordingly, regions in the fusiform gyrus, such as within the FFA complex, are tuned to a broad category of faces (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000), specially when these are presented in central vision, but they do nevertheless also respond to peripherally presented faces (Faivre, Charron, Roux, Lehéricy, & Kouider, 2012; Kanwisher, 2001; Morawetz, Baudewig, Treue, & Dechent, 2010).

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Subcortical regions such as the amygdala are also involved in face meaning extraction (Atkinson & Adolphs, 2011; Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007). This structure, which has been implicated in the detection of external threats (e.g. snakes) (Öhman, 2005) and other ecologically relevant stimuli categories (Sander, Grafman, & Zalla, 2003), receives direct input from temporal visual areas (Lori et al., 2002; Rolls, 2007; Stefanacci & Amaral, 2002) such as the fusiform gyrus (e.g. Faivre et al., 2012), which in turn receives significant input from occipital visual areas (McDonald, 1998), biased for central vision (Strasburger & Jüttner, 2011; Kanwisher, 2001). In any case, the role of the amygdala in processing social aspects of emotion such as in recognition of facial expressions is undisputed (Buchanan et al., 2009; Whalen et al., 2009). In line with this view both invasive and non-invasive studies have previously shown that it responds strongly to human and even animal faces (Blonder et al., 2004; Mormann et al., 2011).

Unsurprisingly, most studies of emotional processing have used central presentation of faces (e.g. Heutink, Brouwer, de Jong, & Bouma, 2011; Morris, Öhman, & Dolan, 1999; Padmala, Lim, & Pessoa, 2010; Vuilleumier, Armony, Driver, & Dolan, 2003; Whalen et al., 2001). However, relevant stimuli that require a rapid response also arise from the visual periphery (e.g. snakes, threatening animals) (e.g. Thorpe, Gegenfurtner, Fabre-Thorpe, & Bülthoff, 2001). In this case, visual input is limited by receptive field properties in the peripheral retina, which are fast but convey mainly coarse information, from the magnocellular pathway (Dacey & Petersen, 1992; but see Atkinson, & Smithson, 2013). Crowding effects and reduced acuity thus weakens the discrimination of fine-grained details (e.g. facial expressions of fear and surprise expressions share many features) (Strasburger, Rentschler, & Jüttner, 2011). Peripheral processing often requires the superior colliculus (SC) and the pulvinar—two structures thought to be involved in a subcortical pathway to the amygdala for fast and often implicit emotional processing (Morris et al., 1999; Vuilleumier et al., 2003), although this is still debated in humans (for recent evidence see Faivre et al., 2012). Due to its role in threat detection, connections with SC and sensitivity to coarse information, it has been suggested that the amygdala might have a bias for peripheral faces (Bayle, Henaff, & Krolak-Salmon, 2009; Palermo & Rhodes, 2007; Preibisch, Lanfermann, Wallenhorst, Walter, & Erk, 2009). In a MEG study, early onset amygdala responses to fearful faces have accordingly been found preferentially at peripheral locations compared to central ones (Bayle et al., 2009). However, such peripheral preference was not found in recent fMRI work (Morawetz et al., 2010; Morawetz, Baudewig, Treue, & Dechent, 2011), and is not consistent with the known major connections with central vision input regions described above (e.g. the fusiform gyrus).

Only a few studies have addressed the neural correlates of central and peripheral processing of facial expressions (Preibisch et al., 2009; Bayle et al., 2009). The pattern of results suggested a complex interaction between facial expression type and spatial location across multiple brain regions (e.g. Preibisch et al., 2009). A magnetoencephalography (MEG) study performed by Liu and Ioannides (2010) found faster peripheral responses but stronger central amplitudes, which is slightly at odds with the study of Bayle et al. (2009). Some of these inconsistencies might be related to differences between tasks. Preibisch et al. (2009) required passive viewing of the emotional faces only, whereas Bayle et al. (2009) masked fearful face stimuli and asked the participants to detect happy faces. Morawetz et al. (2010) manipulated both attentional load (high, low) and task type (implicit or explicit emotion). Finally, Liu and Ioannides (2010) explicitly required participants to verbally name the emotion displayed.

Studies suggesting the existence of specific pathways for implicit and explicit emotional processing have also generated another longstanding debate, with no consensus if the amygdala is preferentially involved when implicit processing of threat is required, or when this emotional information is the focus of attention (explicit processing). Some studies have suggested that explicit labelling recruits cortical temporal and frontal regions thus inhibiting activity of subcortical structures such as the amygdala, which are more prone to respond when the task requires only matching of faces (Hariri, Bookheimer, & Mazziotta, 2000), gender classifications (Critchley et al., 2000) or passive viewing (Morawetz et al., 2010; Taylor, Phan, Decker, & Liberzon, 2003; for a review see Costafreda, Brammer, David, & Fu, 2008). Nevertheless, some studies have found significant engagement of the amygdala during both during implicit and explicit tasks (Winston, O′Doherty, & Dolan, 2003), or even enhanced activity of the left (Gorno-Tempini et al., 2001) or bilateral amygdala (Habel et al. 2007; for a review see Fusar-Poli et al., 2009) when explicit emotional processing is required.

Subcortical structures beyond the amygdala such as the basal ganglia have not been as widely studied as the amygdala in terms of its role in visual processing of affective information. However, they have been implicated in affective processing (Arsalidou, Duerden, & Taylor, 2012), namely but not exclusively in the processing of disgust in faces (Sprengelmeyer et al., 1997). These regions connect with the amygdala in both monkeys (Fudge, Kunishio, Walsh, Richard, & Haber, 2002) and humans (Kim & Whalen, 2009), and show parallel activations with the amygdala in studies of human reward and goal-oriented behaviour (O′Doherty, 2004). Our recent study in a clinical model of basal ganglia dysfunction also suggests a contribution of the basal ganglia in general face emotion recognition (van Asselen et al., 2012).

Concerning explicit vs. implicit processing activity within the basal ganglia, it seems to be modulated by task, with the left putamen showing stronger responses to fearful than to neutral faces during passive viewing, but to neutral than to fearful during explicit emotion judgments (Lange et al., 2003), although another study suggested its involvement both during explicit or implicit discrimination of angry and happy faces (Critchley et al., 2000). In addition, the right neostriatum (putamen and caudate) was activated when subjects made explicit judgements of disgust, with the right caudate (head) differentiating between disgusted and happy faces (Gorno-Tempini et al., 2001) or being generally involved in explicit judgements (Fusar-Poli et al., 2009).

In sum, the role of amygdala in emotion processing does remain controversial (for reviews see Öhman, 2009; Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010) and the link with basal ganglia function remains also intriguing. Here we studied animal face recognition and threat detection using stimuli presented either at foveal regions or at near-periphery locations ($<10^\circ$), although we will refer here to the near-periphery as peripheral vision (see also Strasburger & Jüttner, 2011).

The main goals of this study were to investigate the neural correlates underlying central and peripheral processing of threat relevant stimuli, and in particular test the peripheral bias hypothesis with stimuli that are ecologically relevant for human emotional cognition (animal faces). We hypothesize that different regions may be recruited for central and peripheral processing of faces, given the likely reorganization of amygdala input from foveally biased areas. Since in primates, faces are preferentially processed in the fovea, we also hypothesize amygdala preference for faces presented at central locations. Additionally, we aimed to study the dissociation