Subcortical amygdala pathways enable rapid face processing

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ABSTRACT

Human faces may signal relevant information and are therefore analysed rapidly and effectively by the brain. However, the precise mechanisms and pathways involved in rapid face processing are unclear. One view posits a role for a subcortical connection between early visual sensory regions and the amygdala, while an alternative account emphasises cortical mediation. To adjudicate between these functional architectures, we recorded magnetoencephalographic (MEG) evoked fields in human subjects to presentation of faces with varying emotional valence. Early brain activity was better explained by dynamic causal models containing a direct subcortical connection to the amygdala irrespective of emotional modulation. At longer latencies, models without a subcortical connection had comparable evidence. Hence, our results support the hypothesis that a subcortical pathway to the amygdala plays a role in rapid sensory processing of faces, in particular during early stimulus processing. This finding contributes to an understanding of the amygdala as a behavioural relevance detector.

Introduction

Rapid detection of salient stimuli in the environment is of crucial importance for the survival of an organism. Humans can infer the valence of environmental cues directly, but they also infer valence from the reaction of others, in particular from their facial expressions. The amygdala contributes to the automatic detection of emotional, social or threatening stimuli (Anderson et al., 2003) or facial expressions (Santos et al., 2011) as well as the subsequent adaptation of behavioural responses (Haubensak et al., 2010). Little is known, however, about how relevant information reaches the amygdala so quickly. One model suggests that visual information about faces or whole bodies – particularly in a fearful or threatening context – is conveyed to the amygdala by a cortical and a subcortical processing route (de Gelder et al., 2004; Morris et al., 1998; Rudrauf et al., 2008; Vuilleumier et al., 2003). This is thought to enable rapid and automatic information processing more so than a resource-dependent cortical route (Tamietto and de Gelder, 2010). Diffusion tensor imaging has provided anatomical evidence for a subcortical visual pathway to the amygdala (Tamietto et al., 2012), and a subcortical route has been shown to be functionally active during auditory information processing (Garrido et al., 2012). However, the functional importance and mechanistic contribution of a subcortical connection has been questioned (Kumar et al., 2012; Pessoa, 2005).

An alternative account suggests that a cortical route alone is sufficient, and the amygdala acts to allocate processing resources (Pessoa and Adolphs, 2010). Thus, the issue of whether a subcortical route to the amygdala is engaged during face processing remains unresolved.

Dynamic causal modelling (DCM) is a powerful approach for testing competing hypotheses about connectivity between brain areas. DCM is based on biologically plausible models of distributed and coupled neuronal dynamics on the millisecond timescale. By inverting these models one can estimate connection strengths and evaluate the evidence for different models of connectivity (Daunizeau et al., 2009; David et al., 2006; Friston et al., 2003). In this study, we used DCM to model magnetoencephalographic (MEG) event-related fields (ERFs) in response to emotional faces to test effective connectivity models of visual processing. Faces evoke a pronounced and well-characterised MEG component over the occipitotemporal cortex (Gao et al., 2012; Xu et al., 2005) and are known to elicit amygdala activity early after stimulus onset (Santos et al., 2011). We hypothesised that a subcortical connection subserves this early amygdala processing and therefore contributes to early ERF components, whereas a cortical model that precludes subcortical connections would only be sufficient to explain later components.

Materials and methods

Participants

Twelve neurologically healthy and naïve participants took part in the study (3 males, 9 females, age range 23–35 years). All participants

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reported normal or corrected-to-normal vision and normal hearing. The experimental procedure was approved by the University College London Hospitals Ethics Committee and written informed consent was obtained from all participants. Participants were remunerated for their time.

Experimental procedure

Whole-head magnetoencephalography (MEG) data were recorded using a CTF 275-channel system with 274 functioning second-order axial gradiometers arranged in a helmet-shaped array. Signals were sampled at 600 Hz. To monitor head position with respect to the MEG sensors, three electrical coils were attached to the fiducials (nasion, and left and right preauriculars). Auditory stimuli were presented binaurally through headphones connected to piezoelectric transducers, which were positioned approximately 1 m below the sensor array. Participants were placed in front of a computer screen in a magnetically shielded room.

As reported in Garrido et al. (2012), participants performed a gender discrimination task on visually presented faces by button press (Fig. 1A). 27 male and 27 female faces with neutral, happy or fearful expressions were presented in random order with a total number of 99 faces per emotional condition. Faces were presented for 7 s each with an inter-trial interval jittered between 0 and 300 ms. In addition, tones were presented via headphones in 700 ms intervals for a period of 70 ms each. The tones were pure sinusoids of a particular standard frequency, sporadically interrupted by tones of a deviant frequency. Tones were not time locked to the onset of the visual stimuli and constituted an incidental oddball paradigm that has been reported elsewhere (Garrido et al., 2012). Participants were instructed to ignore the auditory stimulation and were repeatedly reminded to fixate the centre of the visual screen at all times. Stimuli were presented with the Cogent 2000 toolbox for MATLAB (http://www.vislab.ucl.ac.uk/cogent.php).

Data pre-processing and analysis

Data were down-sampled to 200 Hz, band-pass filtered from 0.5 to 30 Hz and baseline corrected with reference to the interval −200 to 0 ms before the onset of visual stimuli. Subsequently, data were epoched with a time window of −200 to 600 ms with 0 ms denoting image onset. Signal contaminated by eye movements or muscular activity was removed using robust averaging as implemented in SPM8 (Wager et al., 2005). Trials were sorted according to emotional valence of the facial expression. Data preprocessing and analysis were performed with SPM8 (Litvak et al., 2011).

To test for differences in peak amplitude between the three emotional conditions, we first conducted paired t-tests over the whole sensor space and all time points to investigate whether fearful faces had a more pronounced ERF than happy or neutral faces. This requires stringent corrections for multiple comparisons. To increase statistical power, we also applied a sensor of interest approach as reported in Xu et al., 2005, which is comparable to a region of interest (ROI) analysis in fMRI. Sensors where the ERF evoked by faces was significantly greater than baseline (P < 0.05) for at least a time window of 25 ms centred on the peak response (and within the time window 0–300 ms) constituted our sensors of interest (SOI). This procedure prevents a bias in
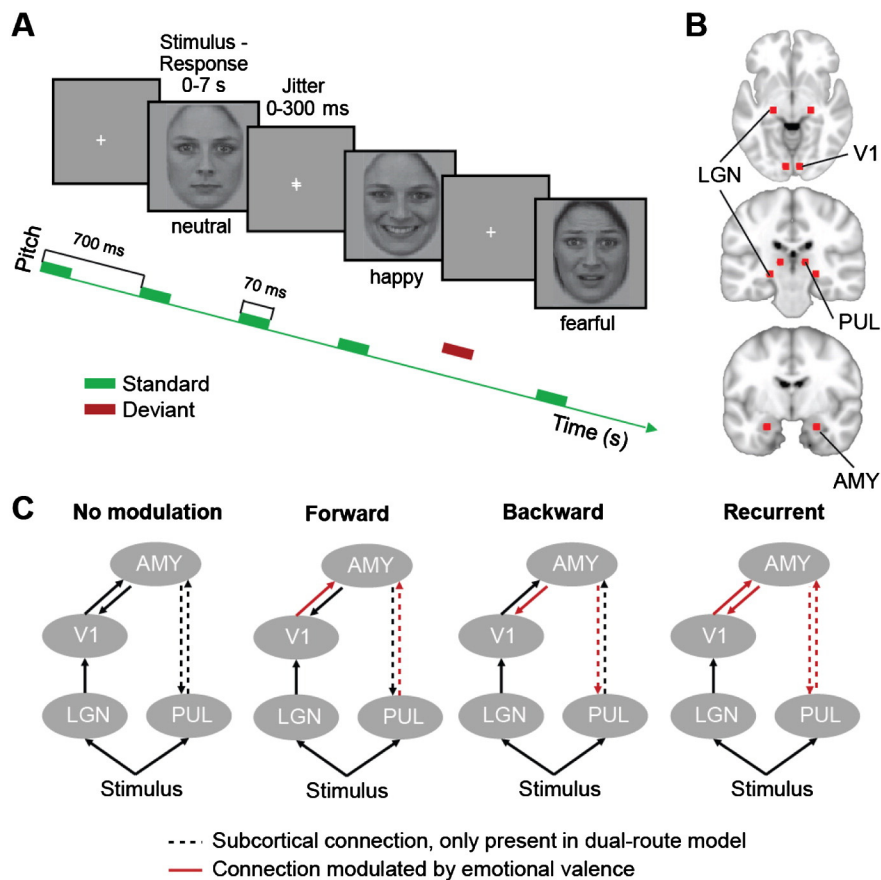

Fig. 1. Behavioural task and DCM architecture. A Task structure. Participants performed a gender discrimination task on neutral, happy, or fearful faces presented in a randomised order. Concurrently, a task-irrelevant sequence of repetitive standard tones (green boxes) occasionally interrupted by deviant tones of higher pitch (red box) was presented binaurally. B Location of equivalent current dipoles included in the DCMs: lateral geniculate gyrus, LGN; primary visual cortex, V1; pulvinar, PUL and amygdala, AMY (See Materials and methods for coordinates). C Two model families were constructed: One family of models comprising a pulvinar–amygdala connection (dual-route models) and one family without this connection (cortical-only models). The dashed line indicates the presence/absence of this subcortical connection. We tested four patterns of modulation by emotional valence for both model families: (1) No modulation, (2) forward, (3) backward and (4) recurrent modulation between pulvinar/V1 and amygdala (indicated by red colouring of the arrows).