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THE TIMING AND DIRECTIONAL CONNECTIVITY OF HUMAN FRONTOPARIETAL AND VENTRAL VISUAL ATTENTION NETWORKS IN EMOTIONAL SCENE PERCEPTION

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Abstract—Electrocortical and hemodynamic measures reliably identify enhanced activity in the ventral and dorsal visual cortices during the perception of emotionally arousing versus neutral images, an effect that may reflect directive feedback from the subcortical amygdala. However, other brain regions strongly modulate visual attention, such as frontal eye fields (FEF) and intraparietal sulcus (IPS). Here we employ rapid sampling of BOLD signal (4 Hz) in the amygdala, fusiform gyrus (FG), FEF and IPS in 42 human participants as they viewed a series of emotional and neutral natural scene photographs balanced for luminosity and complexity, to test whether emotional discrimination is evident in dorsal structures prior to such discrimination in the amygdala and FG. Granger causality analyses were used to assess directional connectivity within dorsal and ventral networks. Results demonstrate emotionally-enhanced peak BOLD signal in the amygdala, FG, FEF, and IPS, with the onset of BOLD signal discrimination occurring between 2 and 3 s after stimulus onset in ventral structures, and between 4 and 5 s in FEF and IPS. Granger causality estimates yield stronger directional connectivity from IPS to FEF than the reverse in this emotional picture paradigm. Consistent with a reentrant perspective of emotional scene perception, greater directional connectivity was found from the amygdala to FG compared to the reverse. These data support a perspective in which the registration of emotional scene content is orchestrated by the amygdala and rostral inferotemporal visual cortex.

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Abbreviations: ANOVA, analysis of variance; FEF, frontal eye fields; FG, fusiform gyrus; fMRI, functional magnetic resonance imaging; FP, frontoparietal; GC, Granger causality; IAPS, International Affective Picture System; IPS, intraparietal sulcus; ROI, region of interest; TR, repeat time.

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INTRODUCTION

Electrocortical and hemodynamic measures reveal enhanced activity in ventral and dorsal visual cortices during emotional relative to neutral picture perception (Pourtois et al., 2004; Sabatinelli et al., 2005; Pessoa et al., 2006; Anticevic et al., 2011; Sabatinelli et al., 2013; Wiens and Syrjanen, 2013), an effect that may reflect a natural selective attention to behaviorally relevant stimuli (Vuilleumier and Driver, 2007; Lang and Bradley, 2010; Pessoa and Adolphs, 2010; Markovic et al., 2013). Some evidence suggests an association between enhanced fusiform gyrus (FG) activity and directive feedback from the subcortical amygdala (Armony and Dolan, 2002; Vuilleumier et al., 2004; Sabatinelli et al., 2005, 2009).

However, other brain regions strongly modulate visual attention, such as frontal eye fields (FEF) and intraparietal sulcus (IPS) (Rizzolatti et al., 1987; Corbetta, 1998; Schafer and Moore, 2007; Bisley and Goldberg, 2010). This frontoparietal (FP) network is persistently involved in a process of categorizing stimulus relevance and directing the locus of visual attention (Corbetta et al., 2008). While the characteristics of this FP network have been thoroughly investigated in target-driven visuospatial attention tasks (Serences and Yantis, 2006) the role of stimulus emotion on the engagement of this network is underexplored. While studies have demonstrated that emotional stimuli evoke augmented FP activity (Moratti et al., 2004; Sabatinelli et al., 2007a,b; Shafer and Dolcos, 2012; Brosch and Grandjean, 2013; Ferri et al., 2013), the mechanisms by which emotional characteristics modulate FP activity are poorly defined (Adolphs, 2002; Mitchell et al., 2008; Vuilleumier and Huang, 2009; Frank and Sabatinelli, 2012).

One means of addressing research questions regarding the temporal order of human brain activity is through comparisons of the relative timing of the BOLD signal within a structure across experimental conditions. While the BOLD signal is inherently delayed and smoothed relative to neural activity, the timing of signal change within active clusters is highly reliable (Kim et al., 1997; Menon and Kim, 1999; Miezin et al., 2000; Lin et al., 2013). Here we sample the BOLD contrast four times per second in 4-slice slabs of ventral (amygdala and FG) and dorsal (FEF and IPS) brain regions during an emotional and neutral picture series to test whether emotional discrimination is apparent in the FP network prior to such emotional discrimination in the amygdala and FG. There is evidence for a rapid response latency in human (Kirchner et al., 2009) and macaque (Schmolesky et al., 1998) FEF, and human data that suggest a role for FEF in modulating attention enhancement in the visual cortex (Taylor et al., 2007). If picture stimulus emotion is discriminated in the FP network prior to the amygdala and FG, a reentrant perspective of emotional perception (Freese and Amaral, 2005; Sabatinelli et al., 2009; Vuilleumier and Huang, 2009) would not be supported. If emotional discrimination is apparent in the amygdala and FG prior to such discrimination in the FP network, the emotionally-enhanced activity seen in FP structures during scene perception may reflect input from the amygdala and FG, or other regions not yet sampled.

Rapid sampling also provides an opportunity to determine potential asymmetries in directional connectivity between structures within the ventral and dorsal networks using Granger connectivity analyses. As there is support for a directive effect of the amygdala on FG (Anderson and Phelps, 2001; Vuilleumier and Driver, 2007; Sabatinelli et al., 2009) and for the FEF on IPS (Bressler et al., 2008), the current data will enable a test of these hypothesized directional connectivities in an emotional picture perception task.

EXPERIMENTAL PROCEDURES

Participants and procedure

Forty-five undergraduate students from the University of Georgia participated in the experiment, receiving $20 USD compensation. Three subjects' data were lost due to MR scanner or stimulus presentation equipment malfunction. Of the 42 participants (average age 22 years, standard deviation (SD) 3) in the final sample, 20 were female. All participants gave informed consent, and this study was approved by the University of Georgia Human Subjects Review Board. All participants reported no neurological abnormalities and had normal or corrected-to-normal vision. Participants were given instructions and provided ratings of pleasantness and emotional arousal of the experimental picture stimuli, printed in booklet form. Prior to entering the bore of the scanner, participants were fitted with earplugs, headphones, fiber-optic goggles (Resonance Technology, Inc., San Diego, CA, United States) and given a patient-alarm squeeze ball. Padding inside the head coil and explicit verbal instruction were used to limit head motion. Each participant spent approximately 45 min inside the scanner, during which they received a structural scan and a series of functional scans. In each functional scan, participants were instructed to attend to each picture and maintain fixation on a red point at the center of the screen throughout the picture series.

Stimuli

Participants viewed a pseudo-randomly ordered series of pleasant, neutral and unpleasant pictures presented in 256 levels of grayscale, at 800 $\times$ 600 resolution, over a 30° horizontal field of view. The picture stimuli depicted categories of content including (1) erotic couples, (2) romantic couples and happy children/families, (3) land/city scapes and people in daily activities, (4) threatening animal and people, and (5) scenes of graphic bodily injury. All stimuli were balanced by category to be statistically equivalent in luminosity using GIMP 2.8 (www.gimp.org). Each participant was presented with four blocks of 20 pictures, with the functional prescription shifting across blocks (described further below). Sixty of the 80 (20 stimuli were omitted due to a computational error) pictures used in the experiment were balanced to be statistically equivalent in joint photographic experts group (JPEG) file size at 90% quality, as a rough gauge of visual complexity. Each picture block began with a 2-s checkerboard acclimation image, followed by a series of 20 experimental picture stimuli presented for 2 s each, interspersed with fixation-only periods of 9–11 s.

Scanning parameters

Once participants were situated inside the magnet, a T1-weighted structural volume was collected consisting of 156 sagittal slices with a 256 $\times$ 256 matrix and 1-mm isotropic voxels. The functional prescriptions were each comprised of four oblique axial slices (64 $\times$ 64 gradient echo planar imaging (EPI), 18-cm field of view (FOV), 5-mm thickness, 1-mm gap, 25° flip angle, 30-ms echo time (TE), 250-ms repeat time (TR)) positioned over slabs of the brain to enable coverage of the amygdala, FG, and substantial regions of calcarine fissure in one prescription, and IPS and FEF in another. The order of prescription sampling was counterbalanced across participants. Each set of four slices was manually positioned using the T1 volume for visual identification of landmarks based on each participant's anatomy. As depicted in Fig. 1, a 4-slice prescription over the amygdala and FG was centered on the amygdala and tilted to abut the border between the ventral temporal lobe and cerebellum. The 4-slice prescription covering IPS and FEF was centered on the IPS and tilted to cover the superior frontal lobe, using cluster locations functionally derived from prior work as a guide (Paus, 1996; Sabatinelli et al., 2007a; Shafer and Dolcos, 2012). Two additional slice prescriptions were acquired but are not presented here.

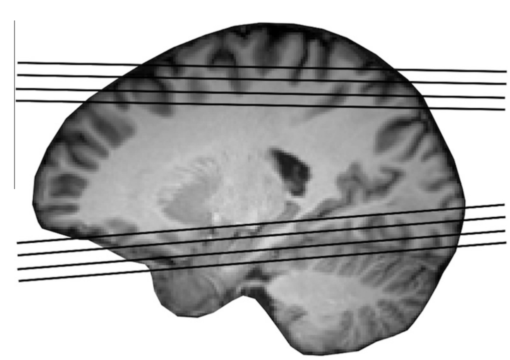

Fig. 1. The approximate location of the 4-slice, 250-ms TR functional prescriptions described in this study.