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Gamma-band activity reflects attentional guidance by facial expression☆

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ABSTRACT

Facial expressions attract attention due to their motivational significance. Previous work focused on attentional biases towards threat-related, fearful faces, although healthy participants tend to avoid mild threat. Growing evidence suggests that neuronal gamma (> 30 Hz) and alpha-band activity (8–12 Hz) play an important role in attentional selection, but it is unknown if such oscillatory activity is involved in the guidance of attention through facial expressions. Thus, in this magnetoencephalography (MEG) study we investigated whether attention is shifted towards or away from fearful faces and characterized the underlying neuronal activity in these frequency ranges in forty-four healthy volunteers. We employed a covert spatial attention task using neutral and fearful faces as task-irrelevant distractors and emotionally neutral Gabor patches as targets. Participants had to indicate the tilt direction of the target. Analysis of the neuronal data was restricted to the responses to target Gabor patches. We performed statistical analysis at the sensor level and used subsequent source reconstruction to localize the observed effects. Spatially selective attention effects in the alpha and gamma band were revealed in parieto-occipital regions. We observed an attentional cost of processing the face distractors, as reflected in lower task performance on targets with short stimulus onset asynchrony (SOA < 150 ms) between faces and targets. On the neuronal level, attentional orienting to face distractors led to enhanced gamma band activity in bilateral occipital and parietal regions, when fearful faces were presented in the same hemifield as targets, but only in short SOA trials. Our findings provide evidence that both top-down and bottom-up attentional biases are reflected in parieto-occipital gamma-band activity.

1. Introduction

Facial expressions are important social cues and may bias attention. Previous work focused on attentional biases towards threat-related stimuli, such as fearful faces, especially in populations with anxiety disorders (Yiend, 2010) and in healthy populations (Cooper and Langton, 2006; Huang et al., 2011) although some evidence suggests that healthy participants tend to avoid mild threat stimuli and exhibit biases towards simultaneously presented neutral stimuli (Bradley et al., 1997; Cisler and Koster, 2010; MacLeod et al., 1986; Mogg and Bradley, 1998). Attentional capture by salient sensory stimuli represents a stimulus-driven bottom-up mechanism of attentional selection. Additionally, top-down control, such as goal-directed attention or task relevance, can bias processing of sensory inputs towards attended stimuli (Desimone and Duncan, 1995). According to an influential model of attentional selection (Corbetta and Shulman, 2002) stimulus-driven attentional processes are mediated by the ventral part of a frontoparietal attention network, whereas top-down control mechanisms are mediated by the dorsal part. Therefore, we expected that attentional guidance by faces involved frontal or parietal brain regions.

Oscillatory neuronal activity may be crucial for the attentional guidance by facial expressions (Engel et al., 2001; Fries, 2009; Siegel et al., 2012). Visual attention concurrently enhances gamma-band activity (> 30 Hz) and decreases alpha-band activity (8–12 Hz) along the visual pathway (Fries et al., 2001; Gregoriou et al., 2009; Müsch et al., 2014; Siegel et al., 2008; Worden et al., 2000). Furthermore, gamma-band activity increases during processing of task-irrelevant fearful faces (Luo et al., 2010). Together, this

Abbreviations: MEG, magnetoencephalography; SOA, stimulus onset asynchrony; MRI, magnetic resonance imaging; ROI, region of interest; FDR, false discovery rate; CSD, cross-spectral density

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suggests that modulation of oscillatory neuronal activity may be involved in the attentional bias to or away from faces, yet direct evidence is missing.

To investigate this, we recorded MEG from a large sample of healthy volunteers and tested if biased attention was associated with changes of oscillatory neuronal activity in the frontoparietal attention network. In a covert spatial attention task participants had to discriminate the orientation of one of two Gabor patches in the left and the right visual hemifield. These target stimuli were preceded by a neutral and a fearful face presented simultaneously on either hemifield. An advantage of our paradigm was that it required a response to a neutral target (Gabor patch) in the absence of any emotional stimulus, discounting general interference effects. Thus effects on target processing could be attributed to the spatial allocation of attention. We hypothesized that, behaviorally, faces influenced target discrimination. On the neuronal level, we hypothesized that attentional biases by emotional face distractors of fearful faces modulated gamma and alpha-band activity in an opposite manner.

2. Materials and methods

2.1. Participants

Forty-eight healthy volunteers participated in this study (normal or corrected to normal vision, no history of psychiatric or neurological illness). Mean state (32.1 ± 5.0) and trait anxiety scores (32.4 ± 5.4), assessed with the Spielberger State Trait Anxiety Inventory, were within the normal range. Four participants had to be excluded from further analysis due to excessive head movement in the MEG (maximal absolute displacement from initial position > 20 mm) leaving a final sample of 44 participants (23 male, mean age 27.1 ± 4.5 years). The average displacement from the origin at the starting position in the remaining sample was 2.6 ± 1.6 mm. All participants provided written, informed consent. The study was approved by the ethics committee of the Hamburg Medical Association and was conducted in accordance with the Declaration of Helsinki.

2.2. Stimuli and experimental procedure

Thirty fearful and neutral faces (15 male, 15 female) from the FACES database (Ebner et al., 2010) were converted to gray-scale, matched for luminance and masked by an oval shape. Gabor patches (sinusoidal gratings in a Gaussian envelope, 2 cpd, 80% contrast) and images of random visual noise were created in MATLAB (MathWorks), serving as targets and visual masks, respectively. Twenty-one Gabor patches (tilted clockwise and counter-clockwise between 0° and 5° from the vertical meridian, steps of 0.5°) were used as distractors. Target Gabor patches were tilted 3° clockwise and counter-clockwise. Face stimuli and their masks subtended $9° \times 12°$, Gabor patches and their masks $9° \times 9°$ visual angle. All stimuli were presented in the upper visual field (3° from the vertical meridian, 6° above the horizontal meridian, viewing distance of 52 cm) at a refresh rate of 60 Hz. Stimulus presentation was controlled using the Psychophysics Toolbox 3 and MATLAB 7.5.0.

All stimuli were presented bilaterally to the left and right visual hemifield to avoid lateralized visual on- and offset responses in the MEG data. After initial fixation (1000–1500 ms) two face distractors (same actor with fearful and neutral expression; 100 ms) were presented bilaterally, followed by two Gabor patches (target and distractor; 100 ms; Fig. 1). As in previous studies investigating the emotional modulation of selective attention (reviewed in: Mogg and Bradley (1998), Yiend (2010)), we presented fearful and neutral faces with straight gaze in each hemifield. Subsequently, a small arrow pointing to the left or right (retro-cue; 100 ms) retrospectively cued the target Gabor patch. Additionally, masks (33 ms) directly followed face distractors and Gabor patches to avoid afterimages. Stimulus onset asynchrony (SOA) between presentation of face distractors and targets was 133 ms (short SOA) or 633 ms (long SOA) to probe allocation of attention at two different time points. Participants indicated the tilt direction of the target by button press with the right index ("left") or middle finger ("right") after a color change of the fixation dot (700 ms after the spatial retro-cue). Responses were delayed to eliminate the impact of button presses on the electrophysiological data during the time interval of interest. Thus, accuracy scores instead of reaction times were analyzed (Van Damme et al., 2008). Participants had to span their covert attention across both hemifields to succeed in the task, because the retro-cue followed the target Gabor patch. Given the fast presentation rate, it is unlikely that participants were able to orient attention towards the target Gabor patch just based on the fixed tilt, thereby neglecting the retro-cue. The overall performance level above chance but well below ceiling supports this notion (see Section 3.1). Furthermore, our paradigm allows assessing the impact of bottom-up driven attentional orienting on top-down directed attentional selection. Please note that saccades could have potentially occurred in the long SOA condition. It is unlikely, however, that this affected the results because participants were explicitly instructed to avoid overt eye movements and needed to covertly attend to the target. This was confirmed by inspection of the electrooculogram which only revealed few saccades.

Ten blocks of 96 trials each were presented in random order, allowing short breaks in between. The first and the second five blocks were recorded separately, allowing for a larger break of about 10 min in between. In total, 120 trials were presented for each of the eight conditions (all possible pairings between $2 \times$ position of the neutral face, $2 \times$ SOA, $2 \times$ tilt direction and $2 \times$ direction of the retro-cue). Facial identities, position of the neutral face, SOA, tilt direction, and direction of the retro-cue were counterbalanced across trials, except for the tilt of the distractor

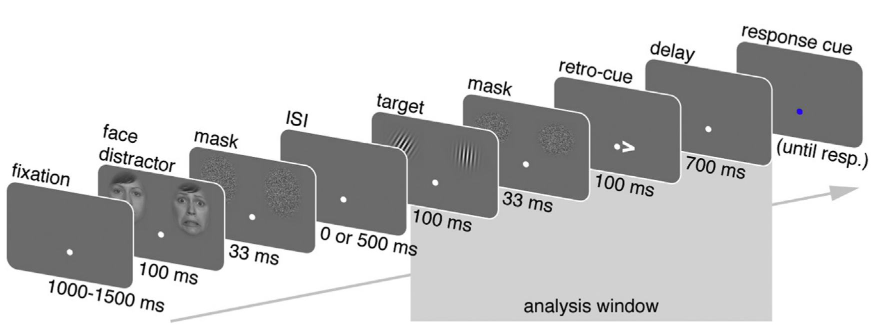

Fig. 1. Experimental design. Participants indicated the tilt direction (left, right) of the Gabor patch denoted by the retro-cue (fixation centered).