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.

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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

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
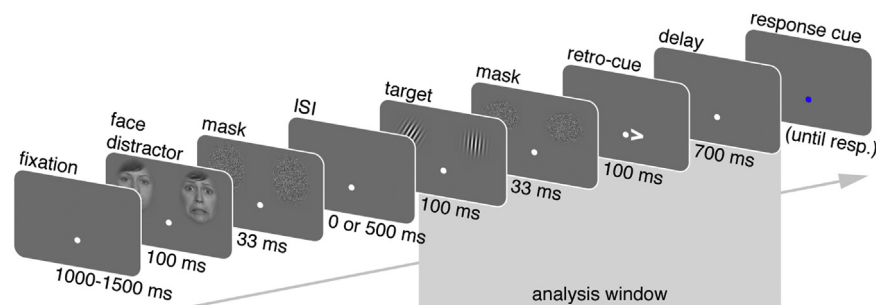

Fig. 1. Experimental design. Participants indicated the tilt direction (left, right) of the Gabor patch denoted by the retro-cue (fixation centered).

patch, which was pseudo-randomized. A gender classification task followed the participants' response ("What was the gender of the face pair in the preceding trial?") in 10% of trials. Importantly, the spatial location and the emotional expression of the faces were irrelevant to the gender classification task. This task probed whether face stimuli were attended.

2.3. Data acquisition

MEG data was acquired with an Omega 2000 whole-head 275-channel axial-gradiometer system (CTF Systems Inc.) at a sampling rate of 1200 Hz (online low-pass filter: 300 Hz cutoff). Four defective MEG sensors were not included in the analysis. Two electrooculogram and two electrocardiogram electrodes simultaneously monitored eye movements and heart beat for offline artifact rejection. Structural T1-weighted magnetic resonance imaging (MRI) scans were obtained with a 3T MR Scanner (Trio, Siemens) for all participants to create individual head models.

2.4. Data analysis

2.4.1. Behavioral data

After discarding premature button presses ($< 20/960$ trials per participant), responses were pooled according to presentation of fearful faces relative to targets (fearful ipsi vs. contra), as the primary interest was the impact of the face distractor on attentional processing. The percentage of correct responses was subjected to a repeated analysis of variance with fearful face (ipsi, contra) and SOA (short, long) as within-subject factors. The percentage of correct responses in the gender classification task was computed for each participant and compared with a paired t-test ($\alpha = 0.05$, two-tailed).

2.4.2. Preprocessing of MEG Data

Analysis of MEG data was performed using MATLAB 8.1.0 and FieldTrip (http://fieldtrip.fcdonders.nl/). Off-line responses were band-pass filtered (0.5–170 Hz; Butterworth; filter order low-pass: 3, high-pass: 4). Line noise was removed (discrete Fourier transform on 10 s continuous data segments removing 0.1 Hz wide bands between 49–51 Hz, 99–101 Hz, and 149–151 Hz). Trials containing muscle artifacts, squid jumps and other non-stereotyped sources (e.g., cars) were removed using semiautomatic artifact rejection. Data were baseline-corrected, resampled (400 Hz) and segmented around target onset (short SOA: -1100 to 1500 ms; long SOA: -1600 to 1500 ms). Extended infomax independent component analysis was applied to remove components representing ocular (eye movements, eye blinks) and cardiac signals. Across all participants, between 2 and 9 components were rejected, which is comparable to previous MEG studies (Hawellek et al., 2013). Artifact correction affected all conditions equally (all Fs < 1.96, all ps > 0.168), resulting in 80–119 trials per condition.

2.4.3. Time-frequency analysis

The analysis focused on the 0–700 ms interval following the onset of the target Gabor patch (analysis window, Fig. 1). Total power was computed using a sliding-window Fourier transformation for each trial with a single Hanning window and three orthogonal Slepian tapers (Thomson, 1982) as sliding windows (20 ms steps) for low (5–30 Hz, 2.5 Hz smoothing, 400 ms) and high frequencies (40–150, 20 Hz smoothing, 200 ms), respectively. Responses were characterized as the percentage of signal change relative to pre-stimulus baseline, avoiding an overlap between baseline and post-stimulus windows.

2.4.4. Statistical analysis

Statistical analysis was performed at the sensor level, and subsequent source reconstruction (see Section 2.4.5) was used to localize the sensor-level effects. We chose this procedure because we were mostly interested in where the sensor-level effects originated from (see Gross et al. (2013)). Statistical analysis was performed in six regions of interest (ROI) at the sensor level excluding the central midline (left/right fronto-central, left/right parieto-occipital, left/right temporal), as strongest effects were expected to be lateralized and occurring over parieto-occipital sensors (e.g., Siegel et al., 2008). The time-frequency information was averaged across all sensors in a ROI. Then, a cluster-based randomization test was applied to each ROI (Maris and Oostenveld, 2007), controlling for multiple comparisons by clustering neighboring samples in time and frequency. More precisely, dependent sample t-tests were calculated within a given ROI for the analysis window at the sensor level (Fig. 1). Adjacent t values exceeding the cluster-level threshold ($\alpha = 0.1$) were combined into a single cluster. Cluster-level statistics were computed by comparing the summed t values of each cluster against a permutation distribution. This distribution was constructed by randomly permuting the conditions (5000 iterations) and calculating the maximum cluster statistic on each iteration. The null hypothesis of no differences between conditions was rejected when $q < 0.05$, after multiple comparisons correction across ROIs with the Benjamini-Hochberg false discovery rate (FDR) control algorithm (Benjamini and Hochberg, 1995).

2.4.5. Source-level analysis

Neuronal activity was source localized at the whole-brain level using DICS linear beamforming (Gross et al., 2001), an adaptive spatial filter technique for time-frequency data. MEG data was recorded relative to the position of three small electromagnetic coils placed on the nasion and left and right periauricular points. Individual structural MRI scans and MEG data were co-registered by aligning those standard anatomical landmarks in both datasets. MRI scans were then segmented, and the brain compartment was used to compute a single-shell headmodel for each of the two MEG recordings (blocks 1–5, blocks 6–10). The individual single-shell headmodel was used to compute the forward model (Nolte, 2003) on a regular 3-D grid (7 mm). Common filters for the conditions of interest (pre-stimulus and post-target interval) were constructed using the leadfield of each grid point and the cross-spectral density (CSD) matrix. The CSD matrix (5% regularization) was computed between all MEG sensors using Hanning tapers (400 ms; 2.5 Hz smoothing) for low frequencies, and Slepian tapers for high frequencies (200 ms; 20 Hz smoothing; 3 tapers). The grid points from each individual structural image were warped to corresponding locations in an MNI template grid (International Consortium for Brain Mapping; Montreal Neurological Institute, Montreal, Canada) before averaging across participants. MNI space coordinates are reported for source-level effects.

3. Results

We computed two types of contrasts: (i) trials with targets presented in the left vs. right hemifield to assess the lateralized attention effect (MEG data), (ii) trials with the fearful face presented in the same (ipsilateral) vs. opposite hemifield (contralateral) as the target to assess the impact of the face distractor on top-down target processing (behavioral and MEG data).

3.1. Behavioral data

As responses in the current paradigm were delayed by 700 ms, reaction times are difficult to interpret. Thus, accuracy scores instead of reaction times were analyzed (Van Damme et al., 2008). We pooled accuracy scores over attention conditions (left + right)

to compare trials with fearful faces presented ipsilaterally or contralaterally to targets (neutral faces in opposite hemifields). Only a main effect for SOA were observed ($F_{(1,43)}=72.38$, $p < 0.001$, $\eta^2=0.68$). In particular, participants were more accurate in detecting the tilt direction in long SOA trials ($M \pm SEM=75.4 \pm 1.6$) compared to short SOA trials ($M \pm SEM=80.6 \pm 1.7$). The position of the fearful face relative to targets did not have an effect (fearful face ipsi: $M \pm SEM=77.8 \pm 1.6$, fearful face contra: $M \pm SEM=78.2 \pm 1.6$), and no interaction with SOA was observed (all $Fs < 0.01$, all $ps > 0.92$). Average performance in the gender classification task was good (short SOA: $M \pm SE=78.29 \pm 1.46$, long SOA: $M \pm SE=72.81 \pm 1.79$) confirming that the participants did not ignore the face distractors. Performance was better in the short SOA condition ($t_{(43)}=4.0$, $p < 0.001$), indicating that participants better remembered the gender of the face when the time interval between presentation of the face distractor and the gender classification task was shorter.

3.2. MEG data

3.2.1. Attentional modulation of neuronal activity

To assess the effect of covert spatial attention during the analysis window (i.e., 0–700 ms interval following the onset of the target Gabor patch), we compared trials with targets presented in the left vs. the right hemifield. The resulting pattern of oscillatory neuronal activity at sensor and source level in the analysis window was clearly lateralized for both SOAs (Fig. 2; same pattern in short SOA). We observed effects in the alpha and beta band (5–25 Hz, 280–700 ms after target onset) and in low and high gamma bands (40–89 Hz and 110–149 Hz, 160–650 ms after target onset). Low

and high gamma-band activity concurrently decreased over left parieto-occipital (long SOA, $q=0.003$; short SOA, $q=0.007$) and increased over right parieto-occipital sensors (long SOA, $q=0.005$, 50–89 Hz, and $q=0.042$, 110–140 Hz; short SOA, $q > 0.05$), as observed with nonparametric cluster-based randomization statistics in the parieto-occipital ROIs (Fig. 2A-B). The power increase in the short SOA did not survive the FDR-correction. In addition, power between 40–89 Hz decreased between 100–450 ms over left fronto-central sensors in the short SOA condition ($q=0.049$, not shown). Source analysis (Fig. 2C) revealed that the low and high gamma-band effects could be attributed to attentional modulations in left and right middle occipital gyri (long SOA: left -36, $-86,10$, right 36, $-86,14$; short SOA: left -24, $-98,2$, right 48, $-78,8$) extending into parietal and temporal areas.

In comparison to gamma-band effects, lateralization of alpha-band effects was reversed and effects occurred later (Fig. 2A-B). Alpha-band activity decreased over right parietal (long SOA, $q=0.022$, short SOA, $q=0.002$) and increased over left parietal sensors (long SOA, $q > 0.05$; short SOA, $q > 0.05$), although the latter did not survive correction for multiple comparisons. The attentional modulation of alpha-band activity peaked in the middle occipital gyri (long SOA: right 42, $-78,18$; short SOA: left -32, $-96,6$; right 48, $-78,6$) and inferior parietal cortex (long SOA: left -32, $-78,44$). Similar to gamma-band effects, alpha-band effects extended into anterior parietal and temporal regions (Fig. 2C).

3.2.2. Biased attention to face distractors

To assess the influence of face distractors on target processing in the time-frequency window of the attention effect (low
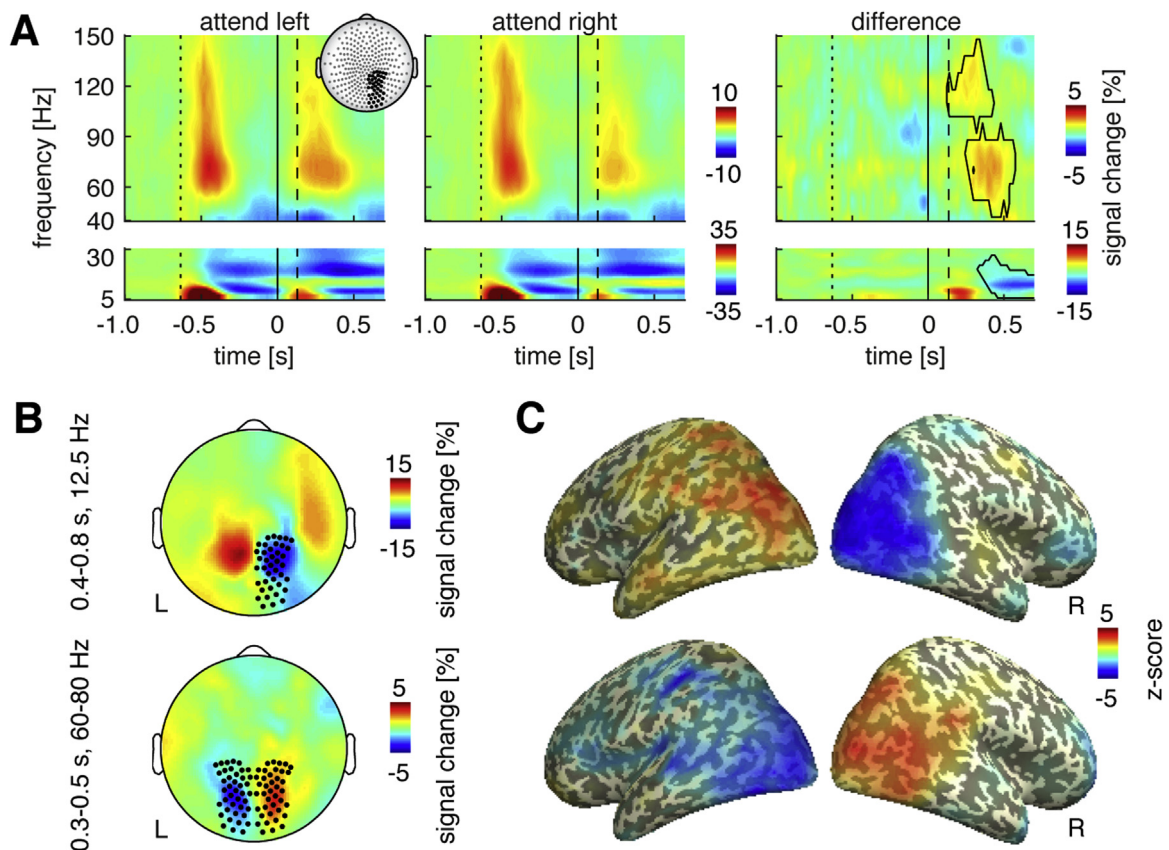

Fig. 2. Lateralized attentional modulation and opposite effects in the alpha and gamma bands. A, Total power changes for "attend left", "attend right" and their difference (right parieto-occipital ROI, inset; dotted line, face distractor onset; solid line, onset of target Gabor patch; dashed line, retro-cue onset; contour lines, statistical difference). B, Topography differences for the same contrast (alpha, top; gamma, bottom; significant sensors highlighted). C, Source reconstruction for the same contrast revealed lateralized attention effects (alpha, top; gamma, bottom) in frontoparietal regions (z-scores).
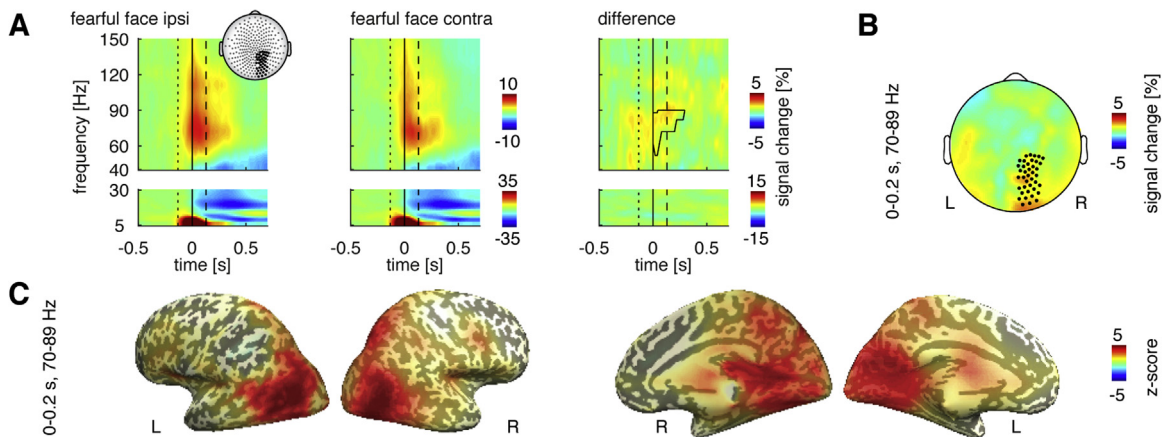
Fig. 3. Biased attention to fearful faces presented ipsilaterally to targets is reflected in changed gamma-band power. A, Increased total gamma-band power in the short SOA condition to "fearful face ipsi" vs. "fearful face contra" (right parieto-occipital ROI, inset; dotted line, face distractor onset; solid line, onset of target Gabor patch; dashed line, retro-cue onset; contour lines, statistical difference). B, Condition difference over right parieto-occipital sensors (significant sensors highlighted). C, Source reconstruction revealed peaks in bilateral parieto-occipital cortices (z-scores).

frequencies: 5–30 Hz, 0–700 ms; high frequencies: 40–89 Hz, 90–150 Hz, 0–700 ms), we compared trials in which fearful faces were presented ipsilaterally to targets with those in which they were presented contralaterally. As this procedure eliminates any effect of lateralization, we do not expect to see the same spatial attention effects as in Section 3.2.1. The neuronal effects can still be attributed to the left or right hemisphere but should be uniform in both hemispheres, rather than opposite.

We observed effects in the low gamma band (60–89 Hz) for the short SOA only (Fig. 3). The analysis of the low frequencies yielded no significant differences for any of the SOAs. For short SOAs, low gamma-band activity significantly increased over right parieto-occipital sensors (60–89 Hz, 0–300 ms after target onset), when fearful faces were presented ipsilaterally to targets ($q=0.034$; Fig. 3A-B). Source reconstruction (Fig. 3C) localized this effect to the left ($-36, -74, 14$) and right ($46, -76, 12$) middle occipital gyri extending into temporal and parietal areas. The sensor-level effect did not correlate with the Spielberger State Trait Anxiety Inventory (all $rs < 0.01$, all $ps > 0.986$).

4. Discussion

The aim of the current study was to investigate if oscillatory neuronal activity mediates attentional guidance by facial expressions. At the behavioral level, we did not find evidence for an attentional bias towards neutral or fearful faces. However, participants more accurately reported the tilt direction, when faces and targets were separated by a 500 ms SOA, supporting the notion that faces interfered with target processing and distracted attention in short SOA trials. At the neuronal level, we found spatially selective, lateralized attentional modulation of gamma and alpha-band activity in parieto-occipital regions in response to visual targets (comparing targets in the left vs. right hemifield). Biased attention towards ipsilateral fearful faces led to enhanced gamma band activity during target processing at an early processing stage in short SOA trials. This effect comprised bilateral occipital and parietal cortices.

4.1. Neuronal basis of spatially selective top-down attention

In line with and extending previous work, spatial attention modulated parieto-occipital gamma and alpha-band activity in a lateralized and antagonistic manner, reflecting the selection of the attended stimulus. Importantly, the oscillatory signatures of attentional processing in our retro-cue paradigm were comparable to previous studies of spatial attention that used classical pre-target cueing. In these studies, in which the spatial cue preceded the target, alpha-band activity was suppressed in the pre-target period, whereas a contralateral gamma-band increase emerged only after stimulus onset (Bauer et al., 2012; Fries et al., 2008, 2001; Siegel et al., 2008; Worden et al., 2000). In contrast, in our task the target was presented before the spatial cue. Thus, participants were required to distribute their attention across both hemifields during target presentation and to subsequently shift their attention to the working-memory representation of the target. For this task, we found both the alpha-band suppression and the gamma-band enhancement around the same time following the retro-cue. Alpha-band suppression has also been linked to working-memory retrieval (Jensen et al., 2002). Thus, our results suggest that directing attention towards task-relevant items in working memory may involve simultaneous alpha-band suppression and gamma-band enhancement. This conclusion receives support from a recent neuroimaging study showing that directing attention to a spatial location in working memory equally accelerated stimulus detection and enhanced activity in parieto-occipital regions as perceptually directing attention to a location in space (Peters et al., 2015).

4.2. Neuronal basis of the attentional bottom-up bias to faces

Gamma-band activity increased in the short SOA trials, when fearful faces were presented ipsilaterally to targets. The manipulation of the SOAs targeted different stages of biasing by the face distractors. That is, face distractors should interfere more with target processing in short SOA trials, which seems to be corroborated by only finding an effect in short SOA but not long SOA trials. These results complement the previously discussed spatial attention effects by isolating attentional biasing signals from the face distractors that interact with the top-down attention effects. The behavioral data also provide indirect support for the assumption that face distractors biased attention in short SOA trials, as performance in the task was lower than in long SOA trials, suggesting that there was stronger interference between face distractors and target processing in short SOA trials. This purely bottom-up driven signal – because face distractors were irrelevant for successful task performance – seems to be short lived, as indicated by the short latency of the gamma-band increase and the absence of a similar effect in long SOA trials. Previous studies also reported enhanced gamma-band power reflecting increased attention (Fries et al.,

2001; Gregoriou et al., 2009; Müsch et al., 2014; Siegel et al., 2008; Worden et al., 2000). Thus, the increased gamma-band power to fearful faces presented ipsilaterally to targets may reflect bottom-up attentional orienting to face distractor processing.

Sources for the attentional facilitation were localized to bilateral occipital and parietal cortices, substantiating the notion that visual processing of face distractors elicited an attentional orienting response. Since the specific contrast (ipsi vs. contra) eliminated any effect of lateralization, the direction of effects should be uniform across the two hemispheres, as illustrated in Fig. 3C. Parietal regions have consistently been identified in attentional control processes (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Serences and Yantis, 2006). Previous work has shown that shifts of visual attention resulted in sustained gamma-band increases in visual cortex and in the ventral intraparietal sulcus after stimulus onset (Siegel et al., 2008) and in frontoparietal regions (Ossandón et al., 2012). Neuroimaging studies employing variants of the cueing paradigm found attentional cueing effects for fearful faces in intraparietal sulcus (Pourtois et al., 2006) and visual cortex (Carlson et al., 2011). Further evidence for the involvement of occipital and parietal regions in attentional orienting to fearful cues comes from two MEG studies, employing images of facial expressions (Lachat et al., 2012) and body postures as emotional distractors (Meeren et al., 2016). Importantly, attentional orienting towards emotional stimuli occurred equally early around 55–80 ms in these MEG studies. Altogether, these lines of evidence support the conclusion that the gamma-band effect in the short SOA condition reflects attentional orienting to face distractors, presumably elicited by fearful faces. Importantly, the present findings provide the first evidence that this orienting response is governed by gamma-band modulations, thereby demonstrating similar mechanisms for bottom-up and top-down attention.

Given that behavioral performance was independent of the position of the fearful face, it is difficult to draw definitive conclusions whether bottom-up attention, as reflected in increased gamma-band power, was biased towards fearful or neutral faces. However, the latency and the associated sources as well as the results from the existing literature allow inferences about the direction of the bias. Gamma-band power increased immediately after onset of the target but before that of the retro-cue, when fearful faces were presented ipsilaterally to targets. Together with the results also showing an early enhancement effect for threat-related stimuli (Lachat et al., 2012; Meeren et al., 2016) we therefore speculate that the gamma-band increase rather reflects a transient attentional bias towards fearful faces, when they are presented on the same side of the target.

An alternative interpretation would be that attention was biased towards neutral faces presented opposite to targets. This interpretation would rather suggest that gamma-band activity reflects attentional avoidance of mild threat stimuli in healthy populations (Bradley et al., 1997; Cisler and Koster, 2010; MacLeod et al., 1986; Mogg and Bradley, 1998). However, this interpretation is rather unlikely for the following reasons. Firstly, if attention was biased towards contralateral neutral faces instead, it has to be rapidly disengaged and allocated to the target in the opposite hemifield for successful task performance. The process of re-allocating attentional control on the target would likely take more time and requires that the position of the target is known. Thus, this attentional re-allocation interpretation is inconsistent with the latency of 0–300 ms, as the position of the target is revealed 133 ms after target onset (due to the latency of the retro-cue). Secondly, refocusing on the task would likely involve more dorsal prefrontal regions or other regions such as the anterior cingulate involved in attentional control (Bishop et al., 2004). Thus, the present results are difficult to reconcile with the assumption of a stronger bias towards neutral faces. Future work will need to elaborate on the present results by presenting two neutral facial expressions, as in other visual probe tasks (Koster et al., 2004), allowing to disambiguate the contribution of attentional bias towards threat relative to attentional avoidance of mild threat in healthy individuals.

4.3. Conclusion

The current study provides new evidence that attentional biases towards task-irrelevant face distractors in a large sample of healthy individuals are exerted through changes in gamma-band activity. This bottom-up driven attentional orienting was independent of lateralized top-down attention effects, showing that top-down and bottom-up processes involve the same oscillatory mechanism. The present results tentatively suggest that attentional orienting is directed towards fearful faces and not neutral faces but this conclusion needs to be corroborated in future work.

Acknowledgements

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