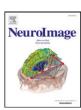


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Neuronal interactions in areas of spatial attention reflect avoidance of disgust, but orienting to danger



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ABSTRACT

For survival, it is necessary to attend quickly towards dangerous objects, but to turn away from something that is disgusting. We tested whether fear and disgust sounds direct spatial attention differently. Using fMRI, a sound cue (disgust, fear or neutral) was presented to the left or right ear. The cue was followed by a visual target (a small arrow) which was located on the same (valid) or opposite (invalid) side as the cue. Participants were required to decide whether the arrow pointed up- or downwards while ignoring the sound cue. Behaviorally, responses were faster for invalid compared to valid targets when cued by disgust, whereas the opposite pattern was observed for targets after fearful and neutral sound cues. During target presentation, activity in the visual cortex and IPL increased for targets invalidly cued with disgust, but for targets validly cued with fear which indicated a general modulation of activation due to attention. For the TPJ, an interaction in the opposite direction was observed, consistent with its role in detecting targets at unattended positions and in relocating attention. As a whole our results indicate that a disgusting sound directs spatial attention away from its location, in contrast to fearful and neutral sounds.

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Introduction

Emotional cues can have a powerful effect on spatial attention. Evolutionary, it seems useful for survival to quickly direct attention towards a dangerous object like a snake in the grass. However, in the case of disgusting stimuli like rotten food or dirty places, it might be better to direct attention away to prevent sickness or infection. Indeed, findings from recent studies suggest that spatial attention is directed towards the location of fearful and angry stimuli but away from the location of disgusting stimuli. When fearful faces or angry sound stimuli were used as spatial cues, participants were faster in detecting emotionally neutral targets when these were presented on the same side as the fearful and angry cues instead of the opposite side (Pourtois et al., 2006; Fichtenholtz et al., 2007; Brosch et al., 2009; Poliakoff et al., 2007). However, the opposite effects were observed with disgust sounds or disgusting faces (Zimmer et al., 2015; Liu et al., 2015; Bertels et al., 2013; Cisler and Olatunji, 2010). Here, participants responded faster when disgust cues were followed by targets on the opposite side of space. Thus, in contrast to fearful and angry cues, disgust cues seemed to be spatially avoided by turning spatial attention away from their

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location. The aim of the present fMRI-study was to investigate the brain areas involved in avoiding disgust, but attending to fear.

To the best of our knowledge, there are so far no fMRI studies which have investigated the redirection of spatial attention when confronted with disgust cues. There are two EEG studies (Zimmer et al., 2015; Liu et al., 2015) that investigated the neural correlates of spatial attention following disgust cues (i.e. facial expressions or sounds) compared with either neutral or fearful cues. Both studies found an emotional modulation of the P300-component which is a positive EEG component occurring roughly 300 ms after a target stimulus is presented. For fearful cues, a P300 was observed that was smaller for targets cued on the same side of space (valid) than on the other side of space (invalid), whereas the reverse was found for disgust cues (Liu et al., 2015; Zimmer et al., 2015). More specifically, the presentation of targets validly cued by disgust (i.e. presented on the same side of space) resulted in a greater P300 compared to targets invalidly cued by disgust (i.e. presented on the opposite side of space). FMRI studies have suggested that the temporoparietal-junction (TPJ) might be one of the possible generators of the P300-component (Kutas et al., 1977; Donchin, 1981; Knight et al., 1989 and Verleger et al., 2005). In the case of non-emotional neutral stimuli, the TPJ typically showed increased activity for invalid compared to valid target positions. This has been interpreted as the TPJ being responsible for detecting targets at invalid positions and redirecting attention to them (e.g. unattended or invalidly cued stimuli; visual: Corbetta et al., 2000; multisensory: Santangelo et al., 2009; Yang and Mayer,

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2014). With respect to disgust stimuli, activation in the TPJ might reflect the redirection of attention away from a disgusting stimulus location. We therefore expect that validity effects in the TPJ reverse when targets are cued by disgust stimuli; that is, greater activity is expected in the TPJ for valid target positions compared to invalid target positions.

Other brain areas might also show an interaction between emotion and validity. FMRI studies investigating spatial cueing effects with emotional cues different from disgust such as fear or anger (Pourtois et al., 2006; Reeck et al., 2012; Carlson et al., 2009) found increased activity in extrastriate visual cortex for validly versus invalidly cued targets. This is similar to studies that used emotionally neutral cues (fMRI: Santangelo et al., 2009; Zimmer and Macaluso, 2007; EEG: Eimer, 2000), as well as to studies that used crossmodal paradigms with neutral cues (Macaluso et al., 2000). Another brain area sensitive to the direction of spatial attention due to cueing is the inferior parietal lobule (IPL). Using fearful facial cues followed by neutral targets, Pourtois et al. (2006) found increased activity in the IPL for validly versus invalidly cued targets. Likewise, in a crossmodal spatial cueing paradigm with neutral cues, Macaluso et al. (2000) found also increased brain activation in inferior parietal cortex next to extrastriate visual cortex. However, it remains to be seen whether the validity effects observed in these areas for neutral stimuli as well as negative emotional cues (anger or fear) reverse in the case of disgust.

In the present fMRI-study, we presented three auditory cues of neutral, disgusting and fearful content intermixed in an event-related spatial cueing design. During fMRI, each of these three sounds was presented equally often to the right or left ear and was followed by a neutral visual target on the same (valid) or opposite (invalid) side of space where the cue was presented. The target was a white arrow, pointing up- or downwards. Participants were required to press one of two buttons indicating whether the arrow pointed up- or downwards. After fMRI-scanning, participants rated all sound cues for emotional valence and arousal as well as their motivation to turn towards or away from a person making such sounds. With regard to the behavioral results, we hypothesized a typical cueing effect for fear and neutral sound cues: a validly cued target should be detected faster than an invalidly cued target. In the case of the disgust cues, however, we expected the reverse pattern: Here, an invalidly cued target should be detected faster than a validly cued target. This would indicate that disgust sounds direct attention away to the opposite side of space, whereas the other two cues should direct attention towards the same side of space. Taken together, the results for fear and disgust should result in an interaction of emotion by validity. With regard to the analysis of the fMRIresults, we expected cue-related activity in auditory cortex independent of emotional types (Ethofer et al., 2012; Zimmer and Macaluso, 2005), but emotion-dependent activation in areas showing some emotion specificity, such as the insula for disgust (Wicker et al., 2003; Brown et al., 2011) and the amygdala for fear (Pessoa et al., 2005; Isenberg et al., 1999). This pattern of results would confirm that, during cuepresentation, the sounds and their emotional context was correctly perceived. For the main analysis of target processing, we expected that the behavioral interaction of emotion by validity would be reflected in areas central to spatial attention, such as the visual cortex and parietal areas like the IPL and the TPJ. Specifically, for the visual cortex and the IPL, we expected more activation when targets were cued invalidly by disgust, but validly cued by fearful and neutral sounds. We hypothesized that this interaction pattern would reverse in the TPJ. Here, more activation should be revealed by targets which are validly cued by disgust, but invalidly cued by fear or neutral sounds.

Materials and methods

Participants

Thirty-two participants (15 men, mean age 26.6 years, SD = 6.3) took part in the fMRI-experiment. All were right-handed, had normal

or corrected-to-normal vision and had no history of psychiatric or neurological disease. For twenty-six of these participants, we included a questionnaire after fMRI-scanning, where we asked them to rate valence and arousal of the emotional sounds and the participants' motivation to turn towards or away from a person making such sounds. In addition, for twelve of the participants, an eye-tracker was available during fMRI-measurements. The recorded eye-tracking data of these participants were used in a second fMRI-analysis, which included only trials with correctly maintained fixation. The participants received course credit for participation, regardless of their performance. All participants gave written informed consent according to the ethical standards laid down in the Declaration of Helsinki (http://www.wma.net/en/30publications/10policies/b3/index.html). The study was approved by the Ethics committee of the University of Graz.

Paradigm

We used a crossmodal spatial cueing paradigm to investigate if disgusting and fearful sound cues would direct spatial attention differently. More specifically, we expected that disgusting sounds would direct spatial attention away from their origin, in contrast to fearful sound cues which should attract spatial attention towards their location. Behaviorally, reaction times to visual targets should be faster for invalid targets compared to valid targets when cued by disgust, whereas the opposite effect was expected for targets cued by fear. This behavioral interaction of emotion by validity should also be reflected in brain activity of the visual cortex. To test this hypothesis, participants had to detect whether a little arrow that was presented either to the left or right side of a centered fixation cross pointed upward or downward. Two thirds of the targets were equally often preceded either by a disgusting or a fearful sound on the same (valid) or opposite (invalid) side of space whereas one third of the targets were preceded by a neutral sound.

Stimuli & fMRI-paradigm

During scanning, a fixation cross was presented at the center of the screen. To the left and right of the fixation cross $(-9.5^{\circ}/+9.5^{\circ})$ horizontally), slightly (4°) below central fixation, two rectangular boxes $(3.5 \times 3.8 \text{ cm}^2 \text{ corresponding to } 3.3^{\circ} \times 3.6^{\circ})$ were positioned. Within these boxes a crowd of little arrows were presented as forward and backward masks (see Fig. 1). For target presentation, the mask was replaced by an arrow, either pointing up- or downwards (50% up/50% down; see also Fig. 1). The side of presentation of the arrow (either to the left or right of the fixation cross) was randomized on a trial-bytrial basis. The emotional cueing sound was one of three different types of sound stimuli (disgust, fear, neutral) which could be presented either to the right or the left ear. The disgust stimulus was a vomiting sound, the fearful stimulus was a female voice screaming in fear and the neutral stimulus was a sound of someone biting into an apple. All sounds were evaluated for valence, arousal and motivation at the end of the fMRI-experiment by most of the participants (see also below). Each of the three sound stimuli had a duration of 1000 ms. This duration guaranteed that the emotional content of the sound was fully processed by the participants before the occurrence of the target (e.g., Paulmann and Pell, 2010). The overall sound level was aligned to 80 dB for both emotional sounds. To conserve the emotional character of the sounds, the time-frequency structures of the original emotional as well as the original neutral sound were not changed (cf. for happy/sad emotional sounds: Banse and Scherer, 1996; Juslin and Laukka, 2001, 2003). For lateralized presentation, the originally stereo-recorded sounds (someone vomiting, screaming fearfully or biting into an apple) were converted into mono-channel sounds by using "Au Adobe Audition" (http://www.adobe.com). During scanning, these mono-channel sounds were then delivered using the software Presentation (neurobehavioral systems; http://www.neurobs.com) to either the left or the right channel of specialized fMRI-headphones that also attenuated the surrounding scanner noise by a noise-reduction level of 30 dB

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