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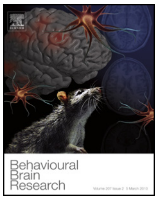

Research report

A frontal attention mechanism in the visual mismatch negativity

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HIGHLIGHTS

- We examine frontal mechanisms underlying the visual mismatch negativity.
- EEG and fMRI activity was examined in respect to unattended oddball stimuli.
- Left inferior frontal gyrus was associated with changes in the stimuli.
- Our findings correspond to similarly implicated regions in the auditory domain.

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ABSTRACT

Automatic detection of environmental change is a core component of attention. The mismatch negativity (MMN), an electrophysiological marker of this mechanism, has been studied prominently in the auditory domain, with cortical generators identified in temporal and frontal regions. Here, we combined electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) to assess whether the underlying frontal regions associated with auditory change detection also play a role in visual change detection. Twenty healthy young adults completed a visual MMN task in separate EEG and fMRI sessions. Region of interest analyses were conducted on left and right middle frontal (MFG) and inferior frontal (IFG) gyri, i.e., the frontal areas identified as potential auditory MMN generators. A significant increase in activation was observed in the left IFG and MFG in response to blocks containing deviant stimuli. These findings suggest that a frontal mechanism is involved in the detection of change in the visual MMN. Our results support the notion that frontal mechanisms underlie attention switching, as measured via MMN, across multiple modalities.

1. Introduction

The Mismatch Negativity (MMN) is an electrophysiological response that reflects the automatic detection of change in the sensory environment, and is elicited by violating an established regularity in a sequence of sensory stimuli. Such violations can take the form of simple physical changes in the stimulus properties (e.g., [47]), abstract deviations in the relationships between stimuli (e.g., [3]), or a non- symmetrical stimulus in a sequence of symmetrical stimuli (e.g., [29]). Since its first description [42] it has become an established tool in the investigation of sensory processing and attention, and a marker of cognitive decline across a variety of conditions (see [43] for a review). After the initial focus on the auditory MMN (aMMN), there is now an established body of evidence for MMN in the visual modality, the vMMN (see [32,34,50,80] for reviews), as well as somatosensory (e.g., [30]) and olfactory modalities (e.g., [36]). Electrophysiological and functional imaging studies suggest a role for both frontal and sensory (temporal lobe) sources of the aMMN (see [10] for review); however, there is limited evidence to date that addresses this question in the vMMN. Thus, the aim of this study was to use both EEG and functional imaging to assess whether a frontal source contributes to the vMMN, which may indicate a multi-modal mechanism for the low-level detection of stimulus change.

Studies of the aMMN have implicated a role for the frontal lobe, with some of the earliest work from Näätänen and Michie [44] suggesting two distinct neural sources underlying the MMN: a superior temporal generator associated with comparison of incoming stim-

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uli with memory traces of previous stimuli; and a frontal generator related to involuntary triggers of attention associated with a change in stimulus. Further work addressed the dissociation of the two proposed neural generators revealing a bilateral (although dominantly right-hemisphere) frontal source in response to infrequent changes in pitch or duration [22,11]. Dipole modeling studies have provided inconsistent evidence for a frontal generator, with most demonstrating that the aMMN can be accounted for by two dipoles located in the superior temporal gyrus (e.g., [58]) with the addition of small, but significant, increases in explained variance with the addition of sources in one or multiple frontal regions. These include the medial frontal gyrus [21], left, right, or bilateral inferior frontal gyrus (IFG; [11,55,59]), and anterior cingulate cortex [26]. fMRI and PET techniques have provided evidence for right IFG activation [39,46] left IFG [40] and bilateral IFG [56,83] following changes in the pitch of acoustic stimuli. Changes in the presentation duration of acoustic stimuli have been associated with increased activation in both the left [39] and right IFG, with some activation also seen bilaterally in the IFG and in regions of the lateral frontal cortex [14,57,59]. This apparent variability in the location of the frontal source may stem from the variations in the degree of attentional focus on the stimuli. Recent work using independent components analysis to examine the oscillatory characteristics of the aMMN has demonstrated that the strength of frontal source responses is modulated by the active or passive nature of a task, as well as stimulus complexity [37].

Given that the aMMN network appears to be comprised of two bilateral auditory cortex sources interacting with a frontal source, it is possible that the frontal source may be involved in the MMN response in other sensory modalities. Recent theoretical and empirical work in the context of the aMMN [19,20], and the vMMN [31,64,65], have discussed the interactions between frontal and sensory areas in the context of hierarchical predictive coding. In this account, the MMN reflects an error signal that is generated when a sensory input does not match a prediction for that input. Frontal mechanisms are thought to underlie the coding of the predicted representation [31,71], which then feeds back to sensory processing regions. Thus, frontal regions are strongly implicated in the vMMN, however, the location and nature of frontal mechanisms has yet to be unequivocally characterized in the literature. There is converging evidence from other paradigms that a frontal mechanism may be sensitive to changes in multiple modalities. Downar et al. [15] used fMRI to examine modality- specific and common networks underlying the passive detection of changes in sensory stimulation in visual, auditory and tactile modalities. Uni-modal activation was observed in visual, auditory, and somatosensory processing areas in respect to each modality, and multimodal activations were observed in a network including bilateral IFG and right insula. Kimura et al., used the spatial modeling technique, sLORETA, for scalp recorded EEG to dissociate any other sources of the vMMN from the visual N1. Frontal activation was found to be associated with the vMMN response in orbital and rectal gyri [33]. A vMMN study using emotional face stimuli implicated a prefrontal mechanism in healthy adults [8]. In another visual deviance detection paradigm, using fMRI to examine responses to infrequent visual stimuli during a visuo-motor tracking task of varying difficulty, activation was observed in the prefrontal cortex, albeit in more medial regions than the lateral activity reported by Kimura et al. [82]. Yucel et al.'s task is somewhat distinct from typical MMN designs in that the primary task has a relatively high cognitive load. This is likely to involve the recruitment of a set of regions which commonly show increased activation in the presence of increased task demands [5,18], as well as dual tasking [35]. These regions also overlap with those implicated as frontal MMN mechanisms, which may moderate the locus of activity observed. Elsewhere, Urakawa et al. [78] used MEG to examine visual deviance detection and demonstrated a large middle occipital gyrus response to infrequent stimuli that was followed by activation in the precuneus and right IFG in three out of eight participants. Finally, an fMRI study of visual change detection in adults with autistic spectrum disorders and healthy adults observed left lateralized frontal and occipital activity [84]. Overall there is a limited but growing body of evidence to suggest a role for frontal areas in visual deviance detection, though its functional role and location are as yet unclear. Specifically, the variation in the cognitive demands of the tasks used in the literature make it difficult to dissociate the mechanisms of low level change detection associated with the vMMN response from processes involved in the active identification of oddball stimuli. The aim of this study was to use the improved localisation of fMRI in conjunction with EEG to investigate the vMMN response to simple visual object change detection without the potential confounding effects of cognitive load.

One line of support is the overlap between the regions implicated as frontal sources for the aMMN and regions associated with the control of visual-spatial attention and cognitive control. In the attention networks framework of Posner and colleagues [53], developed primarily from work on visual-spatial attention, the left IFG has been associated with maintaining a state of alertness to incoming stimuli, and both left and right IFG with an executive attention network [16]. The right IFG has featured prominently in accounts of the mechanisms underlying cognitive control [1]. Recent findings suggest that subregions of right inferior frontal cortex perform distinct roles, with the more dorsal inferior frontal junction acting to detect cue changes, and the IFG supporting the consequent updating of a current action plan in response to these cues [25,79]. Mirroring the findings from aMMN paradigms, whilst a strong emphasis has been placed on the role of the right IFG in these tasks, left or bilateral IFG involvement has been implicated by imaging and lesion studies (e.g., [73,74], for review). A full account of the debate surrounding the role of the IFG in executive control is beyond the scope of this paper, and caution should be taken when drawing inferences about functions across paradigms, though this work highlights a role for this region more broadly in theories of attention. Moreover, the infrequent cues that required detection and behavior adaptation in the studies mentioned were visual, which suggests that if they underlie change detection in the aMMN, they may also be involved in the vMMN.

To examine the potential role of frontal mechanisms in the vMMN, we adapted a variant of a visual mismatch task that has been reported previously in the literature [63,69,77] to be used within a block design functional magnetic resonance imaging (fMRI) study. In addition to having participants perform the task in a separate EEG session, we counterbalanced the combination of visual stimuli used, to verify that any effects observed reflected attentional, rather than stimulus specific, mechanisms. Regions of interest for analysis were derived from the common frontal areas showing activation across 15 fMRI and PET studies examining the neural sources of the aMMN reviewed by Deouell [10].

2. Methods

2.1. Participants

Twenty healthy younger adults (aged 21–34, mean age 25.1 (±4.5), 7 males) took part in the study. Participants gave their informed written consent prior to participation in accordance to the Declaration of Helsinki, and the experiments were approved by the local Ethics Committee. Participants were recruited from the University of Bristol student population, had no known neurological or psychiatric disease, and declared themselves to have normal or corrected to normal vision, and self-reported as being right-hand