

Superior temporal and inferior frontal cortices are activated by infrequent sound duration decrements: An fMRI study

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Received 25 June 2004; revised 1 December 2004; accepted 14 January 2005
Available online 3 March 2005

Functional magnetic resonance imaging (fMRI) was used to examine the processing of infrequent changes occurring in an unattended sound sequence. In event-related brain potentials (ERPs), such sound changes typically elicit several responses, including an enhanced N1, the mismatch negativity (MMN), and the P3a. In the present study, subjects were presented with a repeating sound of 75 ms in duration, which was occasionally replaced, in separate blocks, by a 15-ms, 25-ms, or 35-ms sound (large, medium, and small change, respectively). In the baseline block, only the frequent 75-ms sound was presented. During the scanning, the subjects were instructed to ignore the sounds while watching a silent wildlife documentary. We assumed that in this condition, the MMN mechanism would contribute more to the observed activation than the other change-related processes. We expected sound changes to elicit fMRI activation bilaterally in the supratemporal cortices, where the electric MMN is mainly generated, and that the magnitude of this activation would increase with the magnitude of sound duration change. Unexpectedly, however, we found that only blocks with medium duration changes (25 ms) showed significant activation in the supratemporal cortex. In addition, as reported in some previous EEG and fMRI studies, contrasts between different levels of sound duration change revealed additional activation in the inferior frontal cortex bilaterally. This activation tended to be greater for the small and medium changes than for the large ones.

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Keywords: fMRI; Superior temporal cortex; Inferior frontal cortex; Auditory change detection; MMN

Introduction

The present study used functional magnetic resonance imaging (fMRI) to examine processing of infrequent sound changes occurring in a repetitive train of unattended sounds. Most of the previous knowledge about brain mechanisms involved in processing of such sound changes is based on electric and magnetic brain responses recorded with electroencephalography (EEG) and magnetoencephalography (MEG), respectively. This research has largely focused on certain components of the event-related brain potential (ERP) such as the N1, mismatch negativity (MMN), and P3a. The N1 (peak latency about 100 ms from sound onset) is generated by a fast change in acoustic energy (e.g., sound onset) and its amplitude is determined by the physical properties of the sound. A large N1 is typically elicited by sounds presented at a slow rate or in the beginning of a stimulus train (Hari et al., 1982; Näätänen and Picton, 1987). In contrast, sounds presented at a fast presentation rate will typically elicit only a small N1. However, if the pitch of a sound in a fast-rate repetitive sequence is occasionally changed significantly (e.g., from 1000 Hz to 2000 Hz), then a slightly enhanced N1 is elicited by these infrequent sound changes (Scherg et al., 1989). It is assumed that this enhancement is due to activation of new non-refractory neural populations. In addition to an enhanced N1, infrequent pitch changes also elicit a subsequent MMN response. The MMN is generated by a mechanism that detects deviations from regular aspects of the ongoing auditory stimulation by comparing the incoming sensory information to a representation formed by the repetitive features in preceding auditory inputs (Näätänen and Winkler, 1999). Such a regular feature could be, for example, a repeating single sound, a repeating tone pattern, or even an invariant higher level relationship between sounds (Näätänen et al., 2001). Thus, it is assumed that N1 and MMN reflect the activation of fundamentally different processes: while the N1 is generated by a fast change in the stimulus energy level (stimulus onset) and its amplitude is determined by the physical properties of the sound, the MMN is elicited by changes

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Available online on ScienceDirect (www.sciencedirect.com).

in (higher-level) representations formed on the basis of repeating auditory information (Näätänen and Winkler, 1999). It has been suggested that both the N1 and MMN mechanisms may trigger involuntary switching of attention to the change in the unattended auditory environment (Escera et al., 2000; Näätänen, 1990). The switch of attention itself is generally associated with the P3a response (Escera et al., 2000). Large and salient changes in unattended sounds are more likely to elicit a P3a than small changes.

Although N1, MMN, and P3a occur in close temporal succession within the first 300 ms from change onset and may even partly overlap in time, dissociation of these components from each other is typically possible due to the millisecond-scale temporal resolution of EEG. However, spatial analysis of the brain sources of these components is often more difficult. Previous studies using EEG and MEG source analysis techniques suggest that N1, MMN, and P3a have at least partially different sources in the supratemporal cortex (STC) and that additional areas in frontal and parietal lobes are likely to be involved in their generation (Alho, 1995; Alho et al., 1998; Escera et al., 1998). In contrast to EEG and MEG, spatial information is directly encoded into the fMRI signal and, therefore, it seems worthwhile to use fMRI to map the generator sources of N1, MMN, and P3a with high spatial accuracy. However, the use of fMRI to investigate the mechanisms underlying these auditory ERP components is challenging for several reasons. First, the temporal resolution of fMRI does not allow one to separate the N1, MMN, and P3a generators from each other in time. Second, the mapping between ERPs and the fMRI signal is not fully understood. Further, the loud noise (>100 dB SPL) associated with fMRI recording (Ravicz et al., 2000) activates the auditory system (Bilecen et al., 1998), may impair the perception of other sounds, and may modulate the activation of N1, MMN, and P3a generators (Novitski et al., 2001).

Most previous fMRI studies focusing on auditory change detection have used relatively large frequency changes to elicit hemodynamic responses (Doeller et al., 2003; Liebenthal et al., 2003; Opitz et al., 1999, 2002; Sabri et al., 2004). The use of a pronounced difference between frequent and infrequent sounds is understandable as the scanner noise might impede the perception of the minute details of sounds. However, as noted above, large frequency changes generate several different ERP components and, therefore, the fMRI signal elicited by such changes may reflect activation of several different functional mechanisms related to stimulus detection, change detection, and involuntary attention.

It could be argued that sound duration decrements could be used in an fMRI study to dissociate N1 and MMN type of activation from each other: such changes do not elicit the N1 enhancement in ERPs as stimulus energy is decreased rather than increased (Näätänen et al., 1989). In a previous study, Mathiak et al. (2002; see also, Kircher et al., 2004) manipulated the fMRI imaging sequence so that the gradient noise could be used to produce frequent (quite complex) stimuli and infrequent sound duration decrements (acquisition of 4 instead of 8 echoes; in addition, infrequent amplitude decrements were produced by lowering the strength of the gradients). These duration decrements elicited activation in the right STC. The authors also recorded magnetoencephalographic (MEG) responses to the same sounds and found that the dipole-modeled sources of MMNm (the magnetic counterpart of the electric MMN) were located in STC within the area of fMRI activation. These results demonstrate that duration decrements can be used in an fMRI study to elicit change-

related activation. It should be noted, however, that the spatial match between fMRI activation and MEG source dipole in STC does not unequivocally prove that fMRI and MEG results are caused by the same functional processes.

A parametric design could be one way to ascertain whether the ERP and fMRI results are due to activation of the same brain mechanism: if ERP and fMRI signals are modulated similarly by the magnitude of sound change, it is likely that the methods are measuring the activation of the same functional unit (Doeller et al., 2003; Horowitz et al., 2002; Opitz et al., 2002). In a recent study, Doeller et al. (2003) used three levels of frequency (500 Hz vs. 667, 833, or 1000 Hz) changes in an event-related fMRI paradigm. Their results showed that the frequency changes were associated with activation in the right STC and that this activation increased with the magnitude of the frequency change. In a separate session, the authors recorded ERPs to the same sounds. The infrequent frequency changes elicited a change-related response consisting of several components including at least MMN and P3a. In addition, it is likely that N1 was enhanced by the frequency changes although the authors do not discuss this possibility. In general, the amplitude of the change-related components in their data seemed to increase with the magnitude of the frequency change (though the authors report variations from this monotonic pattern). Thus, it is probable that not only the MMN but also the N1 and P3a generator mechanisms contributed to their fMRI results. Furthermore, the activation of attention-related systems is very likely as their subjects did not have any specific task to engage their attention during fMRI scanning.

In addition to STC activation, Doeller et al. (2003) reported fMRI activation in the bilateral inferior frontal cortex (IFC). This activation was not seen in statistical parametric maps (SPMs) comparing infrequent vs. frequent sounds but was revealed by comparisons between different levels of frequency changes. Frontal activation associated with processing of infrequent sound changes has also been reported by other recent fMRI (Opitz et al., 2002; Schall et al., 2003) and positron emission tomography (PET; Dittmann-Balcar et al., 2001; Muller et al., 2002) studies. Previously, frontal lobe contribution to the electric MMN has been suggested based on EEG (Baldegeweg et al., 2002; Giard et al., 1990; Rinne et al., 2000) and intra-cranial recordings (Liasis et al., 2001). However, the functional role of the frontal lobes in processing of infrequent sound changes and generation of MMN remains poorly understood.

In the present study, we used a three-level parametric design with duration decrements. We presented our subjects with a repeating 75-ms sound (onset-to-onset interval 300 ms) which was occasionally replaced, in separate blocks, by a 15-ms, 25-ms, or 35-ms sound (large, medium, and small sound change, respectively). During the baseline condition, only the 75-ms sound was presented. fMRI scanning was structured so that 1 s of imaging, associated with scanning noise, alternated with a 2.9-s silent period. Most of the frequent sounds and all the infrequent sound duration decrements were presented during these silent periods. During the scanning, subjects were instructed to ignore the sounds while watching a silent wildlife documentary. We assumed that in this paradigm, the MMN mechanism would be activated and would contribute to the observed fMRI signal relatively more than the other possible change-related processes such as those underlying N1 (when stimulus energy is decreased, an enhanced N1 should not be elicited) and P3a (the subjects concentrated on watching a video while ignoring the meaningless sounds). We expected that

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