

Attention Modulates Earliest Responses in the Primary Auditory and Visual Cortices

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SUMMARY

A fundamental question about the neural correlates of attention concerns the earliest sensory processing stage that it can affect. We addressed this issue by recording magnetoencephalography (MEG) signals while subjects performed detection tasks, which required employment of spatial or nonspatial attention, in auditory or visual modality. Using distributed source analysis of MEG signals, we found that, contrary to previous studies that used equivalent current dipole (ECD) analysis, spatial attention enhanced the initial feedforward response in the primary visual cortex (V1) at 55–90 ms. We also found attentional modulation of the putative primary auditory cortex (A1) activity at 30–50 ms. Furthermore, we reproduced our findings using ECD modeling guided by the results of distributed source analysis and suggest a reason why earlier studies using ECD analysis failed to identify the modulation of earliest V1 activity.

INTRODUCTION

Our senses are continuously flooded by stimuli, so much so that we lack the neuronal resources to exhaustively analyze them all. Attention is the umbrella term for mechanisms that select and focus our brain resources on the subset of stimuli that are either perceptually salient or relevant to the current behavioral goal. Attention facilitates perceptual processing of the selected sensory stimuli by modulating the neural processing of incoming sensory signals (Posner and Dehaene, 1994). Notably, selective attention enhances brain responses elicited by attended stimuli (Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000).

Detecting the presence or absence of a stimulus in a target location is an essential task for survival. In order to facilitate the detection, attention may be voluntarily directed to selected locations in space. A fundamental question about the brain mechanisms of this spatial selective attention, which can operate in both auditory and visual modalities, concerns the earliest sensory processing stages that it can affect (Hoermann et al., 2000; Martinez et al., 1999; Noesselt et al., 2002). In selective listening tasks, the earliest modulation of auditorily evoked electrical and magnetic responses by the selective attention to one ear

has been identified in the 20–50 ms poststimulus time interval (Rif et al., 1991; Woldorff et al., 1993). Using ECD analysis of MEG signals, the source of this modulation has been localized in the vicinity of Heschl's gyrus. The estimated location (Rademacher et al., 2001) and latency range (Godey et al., 2001) of this modulation strongly implicate A1 in its generation and suggests an involvement of selective attention at the initial stages of auditory cortical processing (Hillyard et al., 1998). Earlier studies of visual attention have suggested that directing attention to a selected region of the visual field enhances the visually evoked P1 component (onset ~70 ms poststimulus), but does not affect an earlier C1 component (onset ~50 ms). By modeling the neural sources of the C1 and P1 ERP components with dipoles located in the striate and extrastriate visual cortices, respectively, studies concluded that the initial feedforward response in V1 is not affected by attention (Clark and Hillyard, 1996; Hillyard and Anllo-Vento, 1998; Mangun et al., 2001; Martinez et al., 1999; Woldorff et al., 1997, 2002). In this view, visual information processing is first modulated by attention at subsequent stages, in V2 (Woldorff et al., 2002) or V3 (Martinez et al., 1999). Whereas, activity in V1 is modulated at later latencies (140–250 ms), by means of delayed feedback from extrastriate visual areas (Di Russo et al., 2003; Martinez et al., 2001; Noesselt et al., 2002).

A recent study in monkeys (McAlonan et al., 2006) has shown that activity in the thalamic reticular nucleus, which has been hypothesized to control the “attentional searchlight” (Crick, 1984), is enhanced by visual attention at ~25 ms after stimulus onset. Such a short latency is temporally well tuned to influence early visual responses in the lateral geniculate nucleus (LGN) (Maunsell et al., 1999), which is the main visual thalamic relay. If the thalamic reticular nucleus affects early visual processing in the LGN, as its anatomical location and direct projections (Crick, 1984; Guillery et al., 1998) suggest, then one may expect that the earliest V1 response will also be affected by attention, contrary to the conclusions of the earlier ERP and MEG studies (Clark and Hillyard, 1996; Di Russo et al., 2003; Hillyard and Anllo-Vento, 1998; Mangun et al., 2001; Martinez et al., 1999, 2001; Noesselt et al., 2002; Woldorff et al., 1997, 2002). Interestingly, attentional modulation, with larger magnitude than in V1, has been found in the human LGN using fMRI (O'Connor et al., 2002). Furthermore, several studies (Kastner et al., 1999; Ress et al., 2000; Shibata et al., 2007; Silver et al., 2007) have shown that the activity in V1 even before the stimulus presentation can be affected by cueing subjects to attend to a particular location in the visual field.

The results of the aforementioned EEG and MEG studies, concerning the lack of attentional influence on the initial stage of visual sensory processing, may have been in part biased by the methods of data analysis. In these studies, current dipoles, either singly or in mirror-symmetric pairs, were fitted to each ERP or MEG signal component in sequence, over time intervals (~30 ms wide) when the signal topography was relatively stable (Di Russo et al., 2003; Martinez et al., 2001). This approach is more consistent with the assumption that early ERP and MEG signal components reflect activity of discrete cortical generators and less so with the results of recent studies showing that multiple visual areas contribute to each ERP component (Foxe and Simpson, 2002). Particularly, the earlier studies that have not found attentional modulation of the initial V1 response have assumed that the C1 component of ERP represents the V1 activity alone (Di Russo et al., 2003), and therefore its source in the ~30 ms interval (onset ~50–60 ms) was modeled with a single dipole, which was localized around the calcarine fissure. Findings from recent human (Foxe and Simpson, 2002; Poghosyan and Ioannides, 2007) and monkey (Bullier et al., 2001; Hupe et al., 2001; Lamme et al., 1998; Schmolesky et al., 1998) experiments have shown that most of the visual cortex is active at this stage of visual processing, and hence a single point-like current source is a poor model of the generators in the ~50–80 ms interval. Such a modeling might lead to an inaccurate estimate of the V1 source location and its response amplitude in different attentional conditions.

In the present study, we used MEG to record brain responses while subjects performed spatial or nonspatial attention tasks, in auditory or visual modality. Neural sources of the MEG signals were identified using magnetic field tomography (MFT) (Ioannides et al., 1990; Taylor et al., 1999), a distributed source localization method, which together with statistical parametric mapping (SPM) has been shown to localize the initial evoked response in V1 with an accuracy of 3–5 mm (Moradi et al., 2003), and the neural sources throughout visual cortex with within 2 mm reproducibility (Poghosyan and Ioannides, 2007).

In our earlier study (Poghosyan et al., 2005), using the same methods, we have demonstrated that foveally directed attention to shape (feature-based visual selective attention) enhances responses in V1 within 100 ms of stimulus presentation. In the current study, we examine the effect of spatial selective attention in the primary auditory and visual cortices. Specifically, we determine whether or not spatial attention influences the first cortical stage of visual information processing, namely the initial feedforward activity in V1.

We found that (1) the early response (30–50 ms) in putative A1 is tonotopically organized and is enhanced by auditory spatial selective attention, (2) the initial feedforward response in V1 is enhanced by visual spatial selective attention, beginning ~55 ms and peaking ~70 ms poststimulus, and (3) attentional modulation of the visual sensory processing starts in V1, and together with the feedforward volley of activation spreads to V2, V3, and other extrastriate visual areas.

We also demonstrate that this early V1 modulation can be obtained using the ECD model, after fixing the V1 dipole to the

location identified by the MFT/SPM source analysis (“MFT/SPM guided” dipole fit). An “unguided” dipole fit, however, failed to identify the early V1 modulation.

RESULTS

Five subjects were presented with a random sequence of auditory and visual stimuli in their left and right ears and lower left and right visual fields, respectively (Figure 1A). Two categories of stimuli were used in each sensory modality: low (at 475 Hz, 500 Hz, and 525 Hz) and high (at 1900 Hz, 2000 Hz, and 2100 Hz) frequency tones in auditory and checkerboards (oriented vertically, tilted at 18° and –18° angles) and faces (with happy, angry, and neutral expressions) in the visual modality (Figure 1B). Subjects were instructed to maintain fixation on a central cross and respond to the covertly attended target by extending the right index finger, as accurately and quickly as possible. In each run, a different target was used, which required subjects to employ a different type of attention (spatial or nonspatial), in either auditory or visual sensory modality. In different runs, the target was the left or right visual field (visual spatial attention), checkerboards or faces (visual nonspatial attention), left or right ear (auditory spatial attention), and high or low pitches (auditory nonspatial attention; Figure 1C).

Performance

The mean hit rate and reaction time across subjects and runs were 97% and 451 ms, respectively. Performance in visual tasks was marginally better than in auditory tasks (hit rate, 99% versus 94%; $F_{1,4} = 7.57$, $p = 0.051$; reaction time, 437 versus 466 ms; $F_{1,4} = 7.34$, $p = 0.054$). The mean hit rates were similar in the spatial and nonspatial attention runs (96% versus 98%; $F_{1,4} = 0.61$, $p = 0.48$). But the reaction times were faster in the spatial attention runs (434 versus 469 ms; $F_{1,4} = 8.72$, $p < 0.05$). Performance in terms of both hit rate and reaction time was not different in the runs where attention was directed to left or right side (hit rate, 97% versus 98%; $F_{1,4} = 2.67$, $p = 0.178$; reaction time, 430 versus 439 ms; $F_{1,4} = 2.14$, $p = 0.218$).

Attentional Enhancements of MEG Signals

Following minimal preprocessing, the MEG signals were averaged for each run and stimulus separately, with respect to the stimulus onset (–100 to 200 ms). Independent of task, auditory-stimulus-related average signals were characterized by three components in 25–55 ms (M25–55), 60–120 ms (M60–120), and 130–190 ms (M130–190) intervals (Figure 2A). These components were prominent at the contralateral temporal sensors (Figure 2B) and were stronger when the stimulated ear was attended (Figure 2C; M25–55: $F_{1,4} = 11.54$, $p < 0.03$; M60–120: $F_{1,4} = 9.79$, $p < 0.03$). In the visual-stimulus-related average signals, two components distributed over the contralateral occipital sensors were identified, in 50–85 ms (M50–85) and 90–140 ms (M90–140) intervals (Figures 2D and 2E). Just as the auditorily evoked signal components, these components were stronger when the stimulated visual field was attended (Figure 2F; M50–85: $F_{1,4} = 16.86$, $p < 0.02$; M90–140: $F_{1,4} = 28.88$, $p < 0.003$). Peak latencies of signal components did not vary with attentional condition, neither for auditory (M25–55:

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