

Voluntary attention changes the speed of perceptual neural processing

Yasuki Noguchi,^{1,3,4} Hiroki C. Tanabe,² Norihiro Sadato,² Minoru Hoshiyama³ and Ryusuke Kakigi¹

¹Department of Integrative Physiology, National Institute for Physiological Sciences, Myodaiji, Okazaki, Japan

²Department of Cerebral Research, National Institute for Physiological Sciences, Myodaiji, Okazaki, Japan

³Department of Health Science, Faculty of Medicine, Nagoya University, Nagoya, Japan

⁴Division of Biology, California Institute of Technology, Pasadena, California 91125, USA

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Abstract

While previous studies in psychology demonstrated that humans can respond more quickly to the stimuli at attended than unattended locations, it remains unclear whether attention also accelerates the speed of perceptual neural activity in the human brain. One possible reason for this unclarity would be an insufficient spatial resolution of previous electroencephalography (EEG) and magnetoencephalography (MEG) techniques in which neural signals from multiple brain regions are merged with each other. Here, we addressed this issue by combining MEG with a novel stimulus-presentation technique that can focus on neural signals from higher visual cortex where the magnitude of attentional modulation is prominent. Results revealed that the allocation of spatial attention induces both an increase in neural intensity (attentional enhancement) and a decrease in neural latency (attentional acceleration) to the attended compared to unattended visual stimuli (Experiment 1). Furthermore, an attention-induced behavioural facilitation reported in previous psychological studies (Posner paradigm) was closely correlated with the neural 'acceleration' rather than 'enhancement' in the visual cortex (Experiment 2). In addition to bridging a gap between previous psychological and neurological findings, our results demonstrated a temporal dynamics of attentional modulation in the human brain.

Introduction

Many studies in neuroscience have shown that an allocation of attention produces the enhancement of neural activity in various visual areas (Desimone *et al.*, 1990; Motter, 1993; Cook & Maunsell, 2002; Reynolds & Chelazzi, 2004). One important but unsolved question is whether attention also induces temporal changes in sensory neural activities. While previous psychological studies indicate that attention makes the visual processing of humans faster (Posner *et al.*, 1980; Carrasco & McElree, 2001), results in the neurological studies on humans, using electroencephalography (EEG) or magnetoencephalography (MEG), are controversial. In both voluntary and reflexive types of attention, most studies denied a possibility that attention accelerates sensory neural activity (Hillyard & Anllo-Vento, 1998; Di Russo *et al.*, 2003; McDonald *et al.*, 2005), whereas a few groups reported a shortening of latency in EEG waveforms induced by attention (Di Russo & Spinelli, 2002; Schuller & Rossion, 2005).

One possible reason for this discrepancy would be an insufficient spatial resolution of previous EEG/MEG techniques. When investigating visual activities, this would produce a confounding of neural signals from the lower and higher visual areas. On the other hand, it is well known that the attentional modulation is generally stronger in the higher than lower visual areas (Cook & Maunsell, 2002; Saenz *et al.*, 2002). Therefore, the confounding of neural signals from the lower

visual areas into EEG/MEG data might have obscured the attentional modulation of the latency occurring selectively in the higher rather than lower visual regions, resulting in an underestimation or oversight of latency changes in some cases.

In the present study, we investigated this issue by combining MEG with a new stimulus-presentation technique. Our technique is based on previous neurophysiological findings that neurons in the higher visual areas (e.g. fusiform and inferior temporal regions) show a 'cue-invariant' response property (Sary *et al.*, 1993; Grill-Spector *et al.*, 1998). The activities of these high-level neurons are not influenced whether shapes of stimuli are defined by luminance or nonluminance cues (e.g. contrast, texture, or motion) from the background. In contrast, neuronal activities in the lower (e.g. V1) areas are strongly attenuated when stimuli are defined by the nonluminance cue, although they show a strong activity to luminance-defined edges (Chaudhuri & Albright, 1997). Taking advantage of this difference in cue-invariance, we used visual patterns defined by static-dynamic contrast of random dot fields (random-dot blinking method, RDB, Fig. 1A), not by the luminance difference. Thus, those RDB visual patterns can activate the higher visual areas without evoking strong responses in the lower regions, providing an ideal approach for discerning whether attention can change temporal profiles of perceptual neural activity.

In subsequent experiments, we initially confirmed a validity of our RDB method using functional magnetic resonance imaging (fMRI) and examined whether the RDB stimulus could induce a significant activity in the higher visual areas while minimizing responses in the

Correspondence: Dr Yasuki Noguchi, ⁴Division of Biology, as above.
E-mail: noguchi@nips.ac.jp

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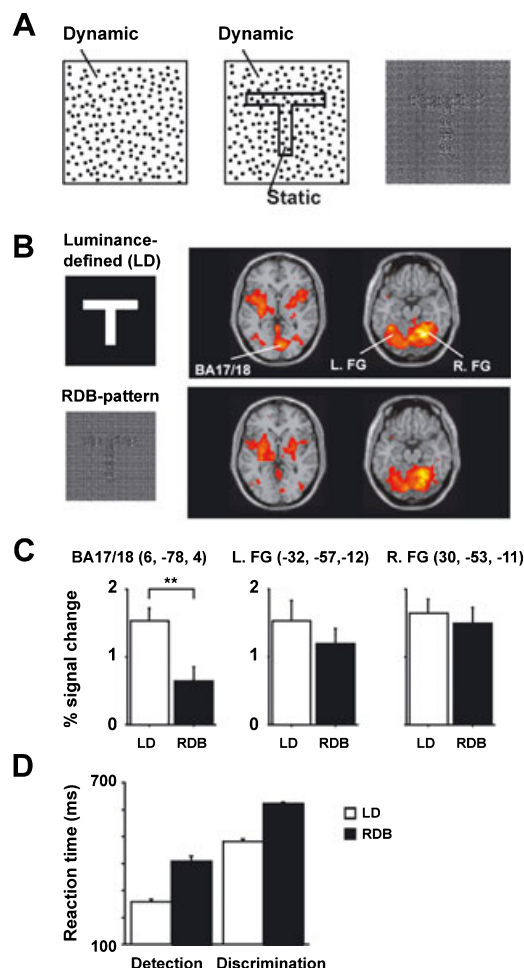


FIG. 1. Random-dot blinking (RDB) method. (A) Schematic illustration of the RDB. While each dot in the field is vibrating at 60 Hz in the resting period (left), the dynamic-static segregation of dots elicits a perception of visual patterns in the presentation period (middle). The actual density of the dot is also shown (right). (B) Brain responses to the presentation of luminance-defined (LD) and RDB letters measured by fMRI. Note that while the activities in the lower visual areas (e.g. BA 17/18) were greatly attenuated in the RDB compared to LD stimuli, neural responses in the higher-visual regions such as the fusiform gyrus (FG) were mostly identical. (C) Comparisons of mean (and SE across subjects) neural activity of the lower (BA 17/18) and higher (FG) visual areas. Talairach coordinates of each region are given in the parenthesis. (D) Reaction time (mean $\pm$ SE across subjects) of the detection and discrimination tasks to the LD and RDB stimuli. $**P < 0.01$.

lower regions. We then applied this technique into two MEG studies, one for a sustained spatial attention and another for a trial-by-trial attention-cuing task.

Materials and methods

Subjects

We conducted four experiments; one fMRI, one behavioural and two MEG experiments. Numbers of subjects were 11 (fMRI), 9 (behavioural), 14 and 10 (MEG Experiment 1 and 2, respectively). All subjects had normal or corrected-to-normal visual acuity. Informed consent was received from each subject after the nature of the study had been explained. All procedures in this study conformed to The Code of Ethics of the World Medical Association (Declaration of Helsinki), and approval for these experiments was obtained from the

ethics committee of the National Institute for Physiological Sciences, Okazaki, Japan.

Random-dot blinking method

All task stimuli in the present MEG study were presented through our random dot blinking (RDB) technique (Okusa *et al.*, 1998; Noguchi *et al.*, 2004), in order to focus on the neural activity in occipito-temporal higher visual regions related to shape perception or object recognition (Grill-Spector *et al.*, 1998; Kourtzi & Kanwisher, 2001). In this method, visual patterns were presented on a black-and-white random dot field (60×60 dots, 8×8 degrees). Although all dots in the field flickered (60 Hz) continuously in the resting period, a subset of dots making up the visual pattern became static during the pattern presentation period while the other dots (outside the visual pattern) remained dynamic (Fig. 1A). This static-dynamic contrast of random dot field enabled observers to perceive the shape of the visual pattern. As the ratio of white and black pixels was fixed (white : black, 1 : 3) throughout both periods, the mean luminance of the field was always the same. According to our previous study, these RDB visual patterns induced one simple neuromagnetic response at a peak latency of 250–300 ms (the 300-ms component), the signal source of which is estimated to lie in the occipito-temporal area around the fusiform gyrus. Other details on the RDB method have been described elsewhere (Noguchi & Kakigi, 2006).

fMRI experiment

Although previous neurophysiological findings on the cue-invariant property in high-level visual neurons (Sary *et al.*, 1993; Grill-Spector *et al.*, 1998; Zeki *et al.*, 2003) lead us to assume that our RDB method could minimize the neural activity from lower visual regions, we examined this assumption using an fMRI technique. Brain responses to the conventional luminance-defined (LD) stimuli and our RDB letters were investigated in separate runs of the block design (Fig. 1A–C). Each run consisted of the alternations of five baseline (20 s) and four activation (24 s) epochs. In the baseline epoch, only the background of each condition (a black screen for the LD and the random-dot field for the RDB runs) was shown and the subjects were asked to fixate on a central point (no task). On the other hand, 12 unilateral stimuli (duration, 300 ms for each) were sequentially presented in the activation epoch at a rate of 2 s per stimulus. The stimuli were either upright or an inverted 'T' (Noesselt *et al.*, 2002) presented at the upper left or right visual field (a centre-to-fixation distance, 4.2 degrees). In the activation epoch of LD runs, upright or inverted white T-shape (34 cd/m^2 , presentation ratio of upright : inverted, 1 : 1) appeared every 2 s with the order of the four types of stimuli randomized. The stimuli were identical in the RDB runs except that the T-shape was depicted by the static-dynamic contrast of the random dots (not luminance difference). In both runs, the subjects were required to judge whether the presented stimuli were upright or inverted, ignoring the position of presentation. They pressed one of two buttons with the right index/middle finger in response to upright/inverted T. One experiment contained four runs, two for LD and two for RDB. The order of the two conditions was counterbalanced across the subjects.

All fMRI experiments were conducted with a 3-T MRI system (Allegra, Siemens, Germany). For functional images, an interleaved T2*-weighted gradient-echo echo-planar imaging (EPI) sequence was used to produce 34 continuous slices of 4 mm thickness covering the entire brain volume (repetition time, 2000 ms; echo time, 30 ms; flip

angle, 75°; field of view, $192 \times 192 \text{ mm}^2$; resolution, $3 \times 3 \text{ mm}^2$). In a single run, 98 volumes were obtained following five dummy images. A three-dimensional whole-head structural brain image of each subject was also obtained using a magnetization-prepared rapid-acquisition gradient echo sequence (Mugler, III & Brookeman, 1990) with the following parameters; repetition time, 2500 ms; echo time, 4.38 ms; flip angle, 8°; field of view, $230 \times 230 \text{ mm}^2$; resolution, $0.9 \times 0.9 \text{ mm}^2$.

The first five EPI volumes of each session were eliminated to allow for the stabilization of the magnetization, and the remaining 98 volumes per session (a total of 392 volumes per participant for four sessions) were used for analysis. Preprocessing and statistical estimation were performed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK) on MATLAB (Math Works, Natick, MA). After realigning EPI volumes for motion correction, the whole-head structural image volume was coregistered with the EPI volume of first scan. Then, the whole-head image was normalized to the Montréal Neurological Institute (MNI) T1 image template using a nonlinear basis function. The same parameters were applied to all EPI volumes. The EPI volumes were spatially smoothed in three dimensions using an 8-mm full-width half-maximum Gaussian kernel. Brain responses to either the LD or RDB stimuli were estimated for each subject using a general linear model with a boxcar waveform convolved with a canonical haemodynamic response function. Group analysis (random-effects model) of each stimulus condition was then performed by entering contrast images into one-sample *t*-test (Friston *et al.*, 1999). Statistical threshold was set at an FDR of $P < 0.05$, corrected for multiple comparisons.

Behavioural experiment

Using the same stimuli as the fMRI session, we conducted a behavioural experiment to estimate a difference in detection times for the LD and RDB stimuli. During a run of one minute, four types of the task stimuli (left upright, right upright, left inverted, and right inverted) were randomly presented at a mean rate of 3 s per stimulus (20 stimuli in each run). The duration of each stimulus was 300 ms and interstimulus intervals (ISIs) between adjacent stimuli were variable (1.5–3.9 s). The subjects were required to do two different tasks on those stimuli; detection and discrimination. In the detection task, they pressed a button as quickly as possible when each stimulus appeared. Both positions and directions (upright or inverted) of the stimuli were irrelevant to this task. In the discrimination task, on the other hand, they had to judge whether the presented 'T' was upright or inverted (presentation ratio of upright : inverted T, 1 : 1), regardless of the position of the stimulus (the same task as the fMRI experiment). They pressed one button as quickly as possible when it was upright and another when inverted. Four conditions, produced by the combination of two stimuli (LD and RDB) and two tasks (detection and discrimination), were tested in separate runs. Each experiment contained eight runs (two runs per condition), with the order of the four conditions counterbalanced across subjects.

Stimuli and task (MEG Experiment 1)

We then applied the RDB method into MEG experiments. During the MEG measurements, subjects maintained a fixation on a centre of the random-dot field (60×60 dots, 8×8 degrees). In Experiment 1, task stimuli are either upright or inverted 'T' (Noesselt *et al.*, 2002) depicted by the RDB method, and presented unilaterally to the locations in the upper left or right visual field (a centre-to-fixation

distance, 4.2 degrees). The locations where the stimuli could appear were demarcated continuously by four small dots (Fig. 2). Each trial block began with an attention-directing cue (duration, 1 s) at the central point (either a left arrow, a right arrow, or a neutral cue indicated by a diamond), followed by a sequence of ten unilateral task stimuli. Each task stimulus lasted 300 ms and ISIs between adjacent stimuli was 1000–1400 ms. Four types of the task stimuli (left or right $\times$ upright or inverted) were randomly intermixed in each sequence, with a constraint that an overall presentation ratio of upright and inverted T was 2 : 8.

In the blocks with the left or right arrow cues, the task of the subjects was to covertly direct attention to the indicated visual field and press a button as quickly as possible when the upright T was presented at the attended hemifield (target detection). They were instructed to neglect all stimuli presented at the opposite visual field. On the other hand, in the neutral blocks with the diamond cue, they pressed a button to the target (upright T) regardless of whether it was presented in the left or right visual field. The subjects performed a total of 54 blocks in one experiment, with the order of three types of blocks (18 for each) randomized. A total of 108 and 432 stimuli were given as the target (upright) and nontarget (inverted), respectively.

Data analyses (MEG Experiment 1)

Visual-evoked fields (VEFs) in response to the task stimuli were recorded with a helmet-shaped 306-channel MEG system (Vectorview, ELEKTA Neuromag, Helsinki, Finland), which comprised 102 identical triple sensor elements. Each sensor element consisted of two orthogonal planar gradiometers (one for measuring latitudinal magnetic fields and another for longitudinal fields) and one magnetometer, providing three independent measurements of the magnetic fields. In the present study, we used MEG signals recorded from 204-channel planar-type gradiometers. The signals from these sensors are strongest when the sensors are located just above local cerebral sources (Nishitani & Hari, 2002). To prevent neuromagnetic artifacts induced by eye blinking, a brief interval (5 s) was interposed every ten stimuli and subjects were asked to blink their eyes within that period. Eye position was also monitored using an infrared eye tracker (Iscan

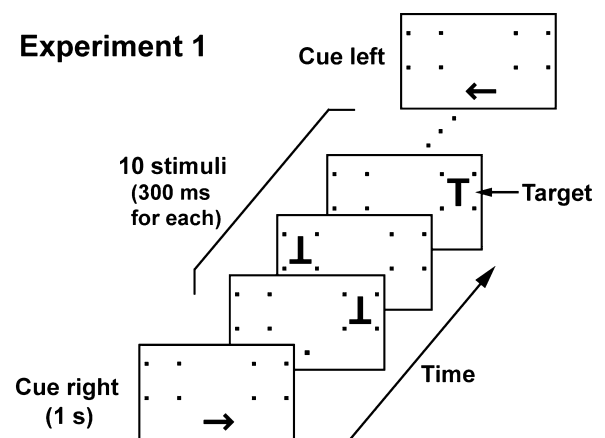


FIG. 2. The target detection task in MEG Experiment 1. One block began with an attention-directing cue (left arrow, right arrow, or diamond indicating the neutral condition) at the fixation, followed by ten task stimuli (upright or inverted T at the right or left upper field). The subjects pressed a button as quickly as possible to the upright T presented at the attended hemifield (both hemifields in the neutral conditions). All visual patterns were depicted by the RDB method in Fig. 1.

Pupil/Corneal Reflection Tracking System, Cambridge, MA), which ensured no systematic eye movements affecting the MEG data in both experiments. The MEG signals were recorded with 0.1–200 Hz bandpass filters and digitized at 600 Hz.

In Experiment 1, we focused on the VEFs to the inverted T letter (nontarget), because our target detection paradigm would induce electromagnetic P300 component to the target (upright T) stimuli (Mangun, 1995) that should be distinguished from the perceptual neural activity in the visual cortex. Two presentation fields (left or right) $\times$ three attentional conditions (attended, neutral, or unattended) of the nontarget stimulus produced six separate VEFs for each subject (number of average, 72 at maximum and 65 at minimum per condition). The averaging epoch ranged from –100 ms to 800 ms after the stimulus onset with the prestimulus period (initial 100 ms) used as a baseline. Epochs in which signal variation was larger than 3000 fT/cm were excluded from the averaging.

To detect the occipito-temporal neural activity in the high-level visual areas (the 300-ms component reported previously), we took the sensor of interest (SOI) approach described in previous MEG studies (Liu *et al.*, 2002; Noguchi *et al.*, 2004). First, apart from the six conditions described above, we averaged MEG responses to all nontarget stimuli ($n = 432$ at maximum and 402 at minimum) for each subject (grand-VEF, Fig. 3A). On this waveform of high signal-to-noise ratio, we selected the SOIs in the present study from 204 planar channels according to the following criteria; (i) the peak deflection was in 200–400 ms after the stimulus onset, and (ii) a significant deflection (> 2 SD of the fluctuation level in the baseline period of each channel) continued for at least 60 ms centering on the peak latency. These criteria were based on our previous results reporting the occipito-temporal activation at a latency of ~ 300 ms (Okusa *et al.*, 1998; Noguchi *et al.*, 2004). An average of 27.8 SOIs were selected for each subject. We then divided these SOIs into two groups (left SOIs and right SOIs), depending on the location of the SOIs on the scalp. As shown in the two delineated fields in Fig. 3A, the SOIs on the posterior left regions were classified as the left SOIs, and those on the posterior right regions were classified as the right SOIs. Sensors on the anterior and midline regions were excluded from the analysis, which allowed us to focus on the neural activity in the lateral perceptual regions of both hemispheres. Using this SOI information, we then averaged original VEFs (separately calculated for the six conditions) across all SOIs within each hemispheric group, producing an across-SOI VEF for each condition of each hemisphere. Because there were two types of SOIs showing positive and negative deflections, VEFs on the negative SOIs were flipped before the across-SOI averaging to match the polarities of all SOIs (Liu *et al.*, 2002). Finally, those across-SOI waveforms in two hemispheres were averaged together, weighted by the number of SOIs in each hemisphere. This between-hemisphere average was conducted according to the stimulus-hemisphere combinations (contralateral or ipsilateral) and attentional states (attended, neutral or unattended). Thus, the across-SOI waveform of the right-attended stimulus in the left hemisphere was paired with that of the left-attended stimulus in the right hemisphere (as a contralateral-attended response), etc. Grand-averaged data of 14 subjects were calculated after all procedures above were applied to each individual data.

In addition to the SOI analyses, we also conducted single equivalent current dipole (ECD) estimations to confirm the anatomical source of the grand-standard VEFs of each subject (Fig. 4A). We adopted a spherical head model based on individual MR images (Hamalainen *et al.*, 1993). The locations of ECDs best explaining the distribution of the magnetic fields over at least 20 channels around the signal maxima were estimated using the least square method. Conforming to the

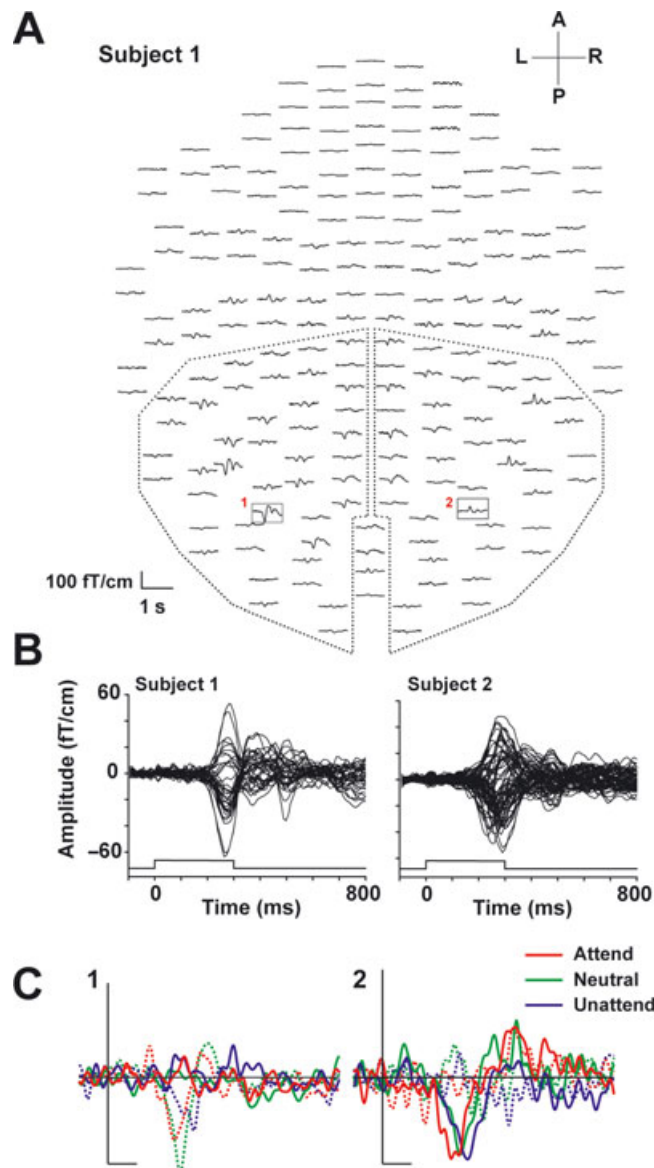


FIG. 3. Visual-evoked fields (VEFs) in representative subjects. (A) Grand-VEF waveforms (see Materials and methods) to the nontarget stimuli over 204 planar sensors. (B) Superimposed waveforms of all SOIs (sensors of interests, see Materials and methods) in Subjects 1 (same as A) and 2. Note that we used an MEG system with 204 planar-type sensors in which a strong neural activity is recorded as large deflections of neuromagnetic curves to either the positive or negative direction. A large neural response was clearly seen in both subjects at a latency of ~ 300 ms (300-ms component). (C) VEFs in two SOIs taken from the data in another subject (the locations of the sensors were marked in panel A). Waveforms in response to the stimuli at the left and right visual fields were shown in solid and dotted lines, respectively. Three lines correspond to the three attentional states (attended, neutral, and unattended). Note the difference in neural latency between the attended and unattended conditions of the contralateral inputs. All waveforms were filtered (0.1–30 Hz) for a display purpose only. Scale bar, 100 ms for horizontal and 100 fT/cm for vertical directions.

criteria in a previous study (Nishitani & Hari, 2002), we accepted only dipoles that accounted for at least 80% of the field variance at the peak. The locations of those ECDs were represented in the head-based coordinate system (Noguchi & Kakigi, 2006). The x -axis in this system was fixed with the preauricular points, the positive direction being to the right. The positive y -axis passed through the nasion and the z -axis thus pointed upward.

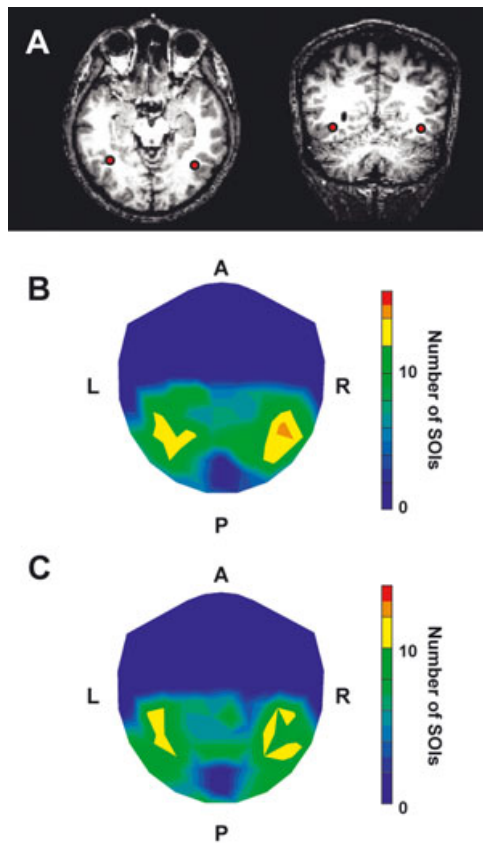


FIG. 4. Anatomical source locations of the 300-ms neuromagnetic response. (A) The equivalent current dipole (ECD) locations estimated at the peak of the 300-ms component in the grand-VEF. The mean coordinates across the subjects were plotted on the MR image of a representative subject. (B) The distribution of 389 SOIs (190 latitudinal and 199 longitudinal) across the 14 subjects in Experiment 1. The number of SOIs in each measurement position was summed across all subjects and colour-coded on a contour map depicted over the topographical layout of 102 sensor positions. Because two types of planar sensors (one for latitudinal and another for longitudinal) were not discriminated, the maximum SOI number in each position was 28 (two sensors per position $\times$ 14 subjects). (C) Same as B, but a distribution of SOIs in Experiment 2 was shown. Note that all figures show a concentration of the 300-ms component around the occipito-temporal regions of both hemispheres.

MEG Experiment 2

In Experiment 2, a representative task of spatial attention (Posner *et al.*, 1980) was reproduced using the same stimulus set as Experiment 1. Each trial consisted of a pair of a cue and a task stimulus (target). After the presentation of the cue (left or right arrow, 300 ms) at the central field, unilateral task stimulus (upright or inverted T, 500 ms) appeared at the upper left or right visual field with a cue-target delay of 600–800 ms. A presentation rate of upright and inverted T was 1 : 1 in this experiment. In 75% of the trials, the task stimulus occurred in the field indicated by the arrow cue (valid trials), while it was presented at the opposite field in the remaining 25% (invalid trials). The task was to report whether the T was upright or inverted by pressing one of two buttons (presentation ratio, upright : inverted, 1 : 1). An important point of Experiment 2 was that the subjects had to respond even when the task stimuli were presented at the unattended field (invalid trials). By investigating the difference in reaction times (RTs) between the valid and invalid trials, we could acquire a behavioural measure of the temporal facilitation by spatial attention. In one experiment, 432 and 144 task stimuli were given as the valid and invalid targets, respectively.

Basic procedures for data analyses were identical to Experiment 1. The VEFs in response to the task stimuli (both upright and inverted T) were calculated (average epoch, –100 to 800 ms), using prestimulus period as a baseline. Two presentation fields of the target and two types of trials (valid and invalid) produced four VEFs; left-valid (number of averages, $n = 216$), left-invalid ($n = 72$), right-valid ($n = 216$), and right-invalid ($n = 72$). Numbers of presentation between the upright and inverted T were equated within each condition so that differences among four VEFs could not be attributed to those in visual features of the stimuli. To evaluate the neural activity in the higher visual regions, the across-SOI waveforms were also calculated, using the grand-VEF ($n = 576$) and the same criteria as Experiment 1. The VEFs in the four conditions were initially averaged across SOIs within each hemisphere, and then collapsed across hemispheres taking the numbers of SOIs into account.

A main purpose of Experiment 2 was to compare the magnitudes of attentional modulation in behavioural and MEG measures. To this end, we calculated an index of attentional modulation (IAM) using the data in the valid and invalid conditions of each subject.

$$\text{IAM} = (\text{invalid} - \text{valid}) / (\text{invalid} + \text{valid})$$

These IAMs were obtained for each of three measures (MEG amplitude, latency, and behavioural RT), and their relationships were investigated by correlation analyses.

Results

fMRI experiment

As shown in Fig. 1B, the LD stimuli induced significant activities in broad regions of the lower visual cortex such as Brodmann area (BA) 17 or 18. As expected, those activities were substantially attenuated in RDB condition, although a small portion of V1 area was found to be significantly activated. On the other hand, activation patterns in the higher visual areas (e.g. fusiform gyrus, FG) were almost identical between the two conditions (Fig. 1B, right). Percentages of BOLD signal changes in the lower and higher visual regions are shown in Fig. 1C. In the BA 17/18, neural activity in the RDB condition was greatly attenuated and became approximately 40% of the LD condition (mean $\pm$ SE across the subjects, LD, $1.53 \pm 0.19\%$, RDB, $0.64 \pm 0.21\%$, $t = 3.76$, $P = 0.0037$). In contrast, activities in the FG were relatively preserved and there were no significant difference of the BOLD signal changes between the LD and RDB in both hemispheres ($t = 0.95$, $P = 0.37$ for left hemisphere and $t = 0.62$, $P = 0.55$ for right hemisphere), showing the cue-invariant activation pattern. These results were consistent with previous studies (Sary *et al.*, 1993; Mysore *et al.*, 2006) and provide the evidence that our RDB method can attenuate the activation in the lower visual areas while retaining the activity in the higher visual regions.

Behavioural experiment

In the detection task, all subjects showed 100% accuracy in both the LD and RDB conditions. Accuracies of the discrimination tasks (mean $\pm$ SE across the subjects) were $98 \pm 0.7\%$ for the LD and $96 \pm 1.0\%$ for the RDB, and there was no significant difference between the two conditions ($t = 1.80$, $P = 0.11$). On the other hand, the RT data were highly differentiated among the four conditions (Fig. 1D). Means $\pm$ SEs across the nine subjects were 258 ± 9 (detection, LD), 410 ± 17 (detection, RDB), 480 ± 11 (discrimination, LD), and 621 ± 8 ms (discrimination, RDB). These results indicate

that the time required for the detection of the RDB stimuli was longer than that of the LD stimuli by approximately 140–150 ms.

MEG Experiment 1 (sustained attention)

Detection rates and RTs of the target (mean $\pm$ SE across the subjects) were $92.7 \pm 1.9\%$ and 625 ± 21 ms when it was presented at the attended field, and $91.7 \pm 1.7\%$ and 621 ± 22 ms when presented at the neutral field (data of one subjects could not be recorded due to a technical reason). No significant differences were observed between the attended and neutral targets (detection rate, $t = 0.53$, $P = 0.61$; RT, $t = 0.47$, $P = 0.64$).

Figure 3A shows the grand-VEF (mean VEF across the six conditions) for one subject over the 204 MEG sensors. Clear MEG responses were observed mainly in sensors on the lateral sides of both hemispheres. Deflections of the MEG signals around the occipital pole were relatively small, indicating that neural activities in the early visual areas were successfully inhibited by the RDB stimulus. Figure 3B shows the superimposed waveform of all SOIs in two subjects. Consistent with our previous study (Okusa *et al.*, 1998), a large neuromagnetic component was observed at a latency of ~ 300 ms (note that, in the planar-type MEG sensors we used, a strong neural activity is represented as large deflections of neuromagnetic curves to either the positive or negative direction). Presented in Fig. 3C are the waveforms of two sensors taken from the data in another subject (their locations were encompassed in Fig. 3A), one in the left and another in the right hemispheres. All six conditions were exhibited and waveforms in response to the task stimulus at the left and right visual fields are shown in the solid and dotted lines, respectively. In addition to the laterality (a greater activity in the contralateral than ipsilateral conditions) of the data, a clear attentional modulation of neural latency was observed in those sensors. The attended stimulus elicited a neuromagnetic response with the fastest peak latency, followed by the neutral and then the unattended conditions.

The results of dipole analyses indicated that all ECDs (equivalent current dipoles) calculated on the grand-VEFs were estimated in the vicinity of the occipito-temporal cortex around the fusiform gyrus, which also confirmed our previous results (Okusa *et al.*, 1998). In Fig. 4A, a mean dipole location of each hemisphere across subjects was shown on the MR image of a representative subject. According to our head-based coordinate system (Noguchi & Kakigi, 2006), the mean coordinates (x , y , z) were $(-38, -24, 51)$ for left and $(41, -26, 51)$ for right hemispheres. No significant difference of the ECD locations was observed between the two hemispheres (x , $t = 0.71$, $P = 0.50$; y , $t = 0.10$, $P = 0.92$; z , $t = 0.01$, $P = 0.99$). When these locations were transformed into the Montréal Neurological Institute (MNI) coordinates, neuromagnetic sources were $(-41, -58, -4)$ in the left and $(42, -62, -2)$ in the right hemispheres, both of which corresponded to the BA 37. These results on the VEF sources were consistent with another topographic map plotting a distribution of 389 SOIs of all 14 subjects (Fig. 4B). This map shows how many times the sensor (either latitudinal or longitudinal) in a certain position was selected as SOI across all subjects. We found that the SOIs were concentrated over occipital-temporal regions of both hemispheres and distributed equally to the left and right hemispheres (193 in the left and 196 in the right).

Fig. 5 shows the across-SOI VEFs (absolute-mean waveforms averaged across all SOIs) of 14 subjects. Both to the contralateral (solid lines) and ipsilateral (dotted lines) inputs, the attended stimulus in the contralateral visual field evoked stronger and faster 300-ms

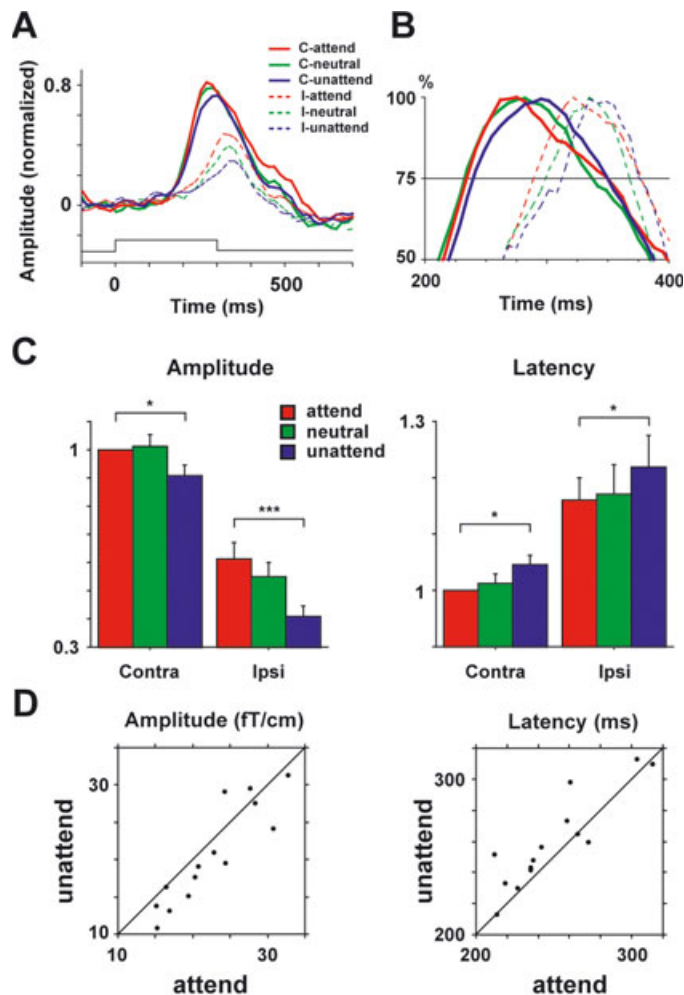


FIG. 5. The attentional enhancement and acceleration effects. (A) Across-SOI VEFs (mean of 14 subjects), shown with the same colour convention as Fig. 3C. Zero in the horizontal axis indicates an onset of the nontarget stimuli (inverted T). Variances in peak amplitude across the subjects were normalized by setting the data in the contralateral-attended condition of each subject as 1. In (B), the timings of increase and decrease of the six waveforms in A were replotted by setting the peak of each waveform as 100%. Note the faster increase of neural activity in the attended than unattended conditions, even when the differences of amplitude were excluded. C, contralateral; I, ipsilateral. (C) Mean and SE (across subjects) of the peak amplitude (left) and 75% latency (right). All amplitude and latency data were normalized (i.e. converted into relative values) to those in the contra-attended condition. Thus, the values of the contra-attended condition were always 1 in all subjects, producing no errors bars in this condition only. * $P < 0.05$, *** $P < 0.001$, paired t -tests. (D) Paired comparisons of contra-attended and contra-unattended conditions in amplitude (left) and latency (right). Each point shows a data of 1 subject, plotted above or below the 45-degree line.

component than the unattended stimulus in the same field. In Fig. 5B, we normalized the peak amplitudes of the six waveforms in Fig. 5A so that the attentional modulation in neural amplitude was excluded from the timeseries. The results revealed that the neural responses to the attended stimulus were faster than those to the unattended stimulus both in the contralateral and ipsilateral hemifields.

We then examined the attentional modulation statistically by calculating the peak amplitude and latency of the across-SOI VEFs in the six conditions for each subject. The latency was defined as the first time point when the neural response reached 75% of its peak amplitude. Repeated-measures ANOVAs of laterality (contralateral vs.

ipsilateral) $\times$ attentional states (attended vs. unattended) with the Greenhouse-Geisser correction indicated greater amplitude ($F = 27.1$, $P < 0.001$) in the attended compared to unattended conditions (Fig. 5C, left), which was consistent with the many previous studies reporting an attentional enhancement. Moreover, our data showed that the neural latency to the attended stimuli was significantly shorter than the unattended ($F = 11.2$, $P = 0.002$), demonstrating a temporal effect of attention in the higher visual cortex (Fig. 5C, right). The results were not changed when the peak (not 75%) latency were compared between the attended and unattended conditions ($F = 17.4$, $P < 0.001$). Figure 5D shows a paired comparison of the contralateral-attended and contralateral-unattended conditions in 14 subjects. In peak amplitude, 12 of the 14 subjects showed higher values in the attended condition and located below the 45-degree line (left, panel), whereas most data were concentrated on the upper field (unattended > attended) in neural latency (right panel).

MEG Experiment 2 (trial-by-trial attention-cueing task)

The results in Experiment 1 showed that the attention changes the speed of sensory neural activity. However, as the RT was not significantly different between attended and neutral targets, it remained to be elucidated whether this increase in the speed of neural activity could be correlated with changes in behavioural measures. We therefore conducted the second experiment using a conventional, trial-by-trial cuing task (Posner *et al.*, 1980) (Fig. 6A). Although accuracies were almost perfect (mean $\pm$ SE across the subjects, valid, $97.1 \pm 0.5\%$; invalid, $96.0 \pm 0.9\%$), this task produced significantly shorter RTs for the valid than invalid trials (valid, 632 ± 20 ms; invalid, 725 ± 20 ms; $t = 5.43$, $P < 0.001$), reflecting the temporal 'benefit' of spatial attention.

We measured the neuromagnetic activity during this task. The SOIs from each subject were selected based on the same criteria as Experiment 1. As shown in Fig. 4C, the topographical distribution of these SOIs was similar between Experiment 1 and 2. Also, no hemispheric lateralization was found in numbers of SOIs (163 in the left and 168 in the right hemispheres), which was also consistent with Experiment 1. These results suggested the common neural sources of the 300-ms component in two experiments. Figure 6B shows the across-SOI waveforms in the four conditions; the contralateral-valid, contralateral-invalid, ipsilateral-valid, and ipsilateral-invalid. Again, the neural activity in the valid trials was observed to be faster than the invalid trials both in the contralateral and ipsilateral hemifields. We summarized in Fig. 6C the peak amplitude and latency in the contralateral valid and invalid conditions. Surprisingly, there was no difference in peak amplitude between the valid and invalid trials ($t = 0.16$, $P = 0.88$, Fig. 6C, left), although the difference in latency remained significant ($t = 2.42$, $P = 0.039$, Fig. 6C, right). We presumed this lack of attentional enhancement was caused by the reorientation process of spatial attention in the invalid trials (see Discussion). When these MEG measures were directly compared with the behavioural RT data, the neural latency showed a significant correlation with the RT ($r = 0.46$, $P = 0.04$), while no correlation was observed between the neural amplitude and RT ($r = -0.36$, $P = 0.12$). Finally, we correlated the IAM (index of attentional modulation) among the three measures (Fig. 6D). Significant correlation with the RT data was selectively found for the neural latency (RT vs. amplitude, $r = -0.11$, $P = 0.77$; RT vs. latency, $r = 0.64$, $P = 0.046$). The results were not changed when the MEG data in the ipsilateral conditions were included into the analysis (RT vs.

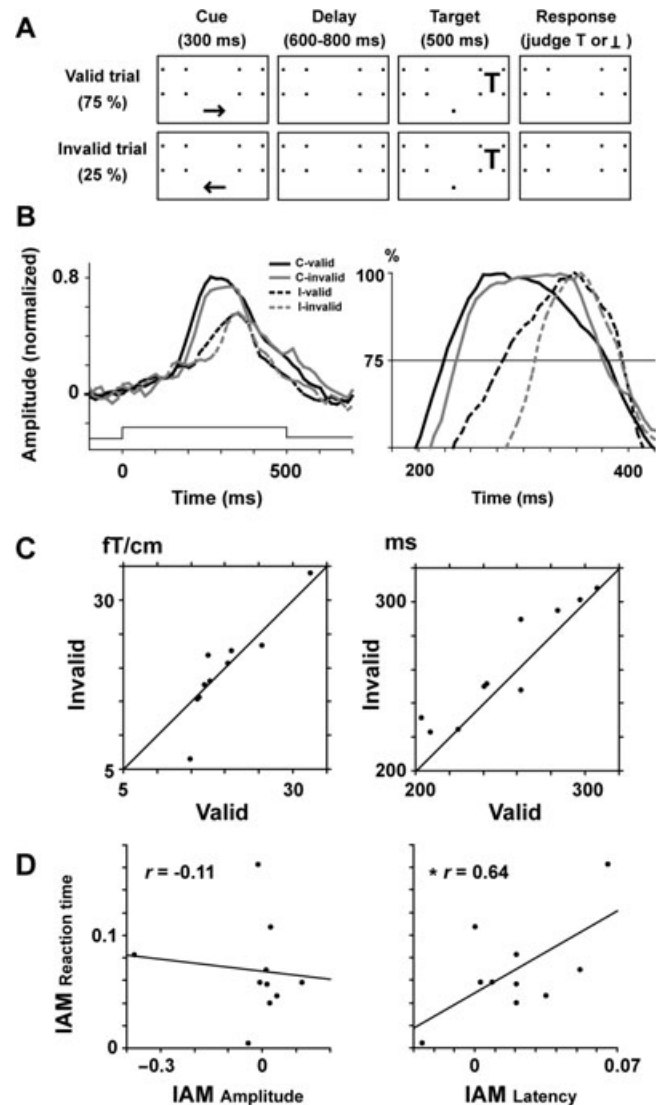


FIG. 6. The task and results in MEG Experiment 2. (A) In every trial, subjects answered the direction of T (upright or inverted) presented after the cue (left or right arrow) predicting the location of the target with 75% accuracy. (B) Across-SOI waveforms (mean of ten subjects) in response to the target. Zero in the horizontal axis indicates an onset of the target. Variances in peak amplitude across the subjects were normalized by setting the data in the contralateral-valid condition of each subject as 1. Note the faster neural responses in the valid (black) than invalid (grey) trials both in contra- (solid) and ipsilateral (dotted) conditions. (C) Paired comparisons of the contra-valid and contra-invalid conditions in neural amplitude (right) and 75% latency (left). A significant effect of validity was observed only in the neural latency ($t = 2.42$, $P = 0.039$, paired t -test). (D) Correlations of the two MEG measures (amplitude and latency) with the RT. Indices of attentional modulation (IAMs) were plotted. Significant correlations with the RT were only observed in the latency. * $P < 0.05$, significance test for correlation coefficients.

amplitude, $r = -0.05$, $P = 0.83$; RT vs. latency, $r = 0.53$, $P = 0.016$).

Discussion

Using the new method to focus on the higher visual regions, the present MEG study provided clear evidence that the voluntary allocation of spatial attention changes the speed of neural activity in

the higher visual regions (MEG Experiment 1). Moreover, the comparison between the MEG and behavioural measures in the trial-by-trial cuing task (MEG Experiment 2) indicated that the attentional decrease of the RT in previous psychological studies was closely related to the change in the latency of visual neural activity.

Attentional acceleration and the gain control theory

The present findings are important in providing a neurological basis for the attention-induced behavioural facilitation, one of the oldest findings in psychology (Titchener, 1908). So far, the lack in temporal modulation of sensory neural activities (despite the clear evidence of behavioural facilitation) has been explained by assuming a gain control mechanism in the brain (Hawkins *et al.*, 1990; Hillyard *et al.*, 1998; Luck *et al.*, 2000; McDonald *et al.*, 2005). In this hypothesis, attention-induced enhancements of neural activity reflect a stimulus processing with high signal-to-noise ratio in the visual cortex. This provides the improved sensory information for the subsequent (e.g. judgement) stages in the brain, enabling accurate and rapid behavioural responses to the attended stimulus. Our results in Experiment 2 are not directly consistent with this view because we observed a close relationship between the shortening in the RT and the change in the latency (not amplitude) of neural activity. However, one should note that our magnitude of latency change was smaller (10–20 ms) compared to the behavioural facilitation (80–90 ms). One possibility explaining this difference is that the magnitude of behavioural facilitation was determined by the neural activity in limited population of the visual cortex where the latency change was most prominent. While the magnitude of latency change was nearly 100 ms in some MEG channels (Fig. 3C), we averaged the data in many MEG sensors over broad regions in the visual area (Fig. 4). This macro-level approach might cause an underestimation of latency change in our data, resulting in the difference between the behavioural and neural measures (although we could observe significant correlations between them in Fig. 6). Another possibility is that a portion of behavioural facilitation (RT reduction) was produced in nonsensory (e.g. judgement or motor) stages in the brain that was not reflected in the VEF waveforms recorded in the present study.

A lack of latency changes in previous EEG/MEG studies on voluntary attention

Although a number of studies using EEG/MEG have investigated the neural timeseries to the attended and unattended stimulus, most of them could not find a reliable change in neural latency induced by attention (Hillyard & Anllo-Vento, 1998; Noesselt *et al.*, 2002; Di Russo *et al.*, 2003; McDonald *et al.*, 2005). We presume this is mainly due to the insufficient spatial resolution of the previous EEG/MEG techniques. As the magnitude of attentional modulation is smaller in the early than late visual areas (Cook & Maunsell, 2002; Saenz *et al.*, 2002), the confounding of early visual signals into MEG data would obscure the small latency change (10–20 ms in the present study) occurring in the higher visual areas. Most of the previous studies reported an attentional modulation of amplitudes in P1 (80–130 ms) or N1 (140–200 ms) components, but the signal sources of those responses were very controversial (Di Russo *et al.*, 2005). Many studies have found a close relationship between the P1 responses and V1 activity (Slotnick *et al.*, 1999; Bonmassar *et al.*, 2001), although others found a maximal P1 waveforms over the lateral occipito-temporal sites (Mangun, 1995; Noesselt *et al.*, 2002). Furthermore, recent studies reported that the V1 area showed a delayed activation at

a partially overlapping latency with the N1 component (140–250 ms), by receiving feedback signals from the higher visual cortex (Noesselt *et al.*, 2002; Halgren *et al.*, 2003). These results indicate a mixture of neuronal signals from the lower and higher visual areas in previous studies on voluntary attention. Our RDB method provided an improved approach to this problem by minimizing a contribution from the lower regions.

Relationships of the 300-ms waveform with P300 or N2pc component

One characteristic of our RDB method is a slow latency of the first VEF component (250–300 ms). This may raise a possibility that the present 300-ms component did not reflect a sensory-evoked neural activity but was related to later EEG/MEG components such as P300 or N2pc (Woodman & Luck, 1999; Hopf *et al.*, 2006). However, several aspects of our data do not support this view. In the first MEG experiment, all VEFs were recorded on the frequently presented (80%) nontarget stimulus (inverted T). The clear 300-ms component was nevertheless observed in both the attended and unattended conditions, indicating that our 300-ms waveform was different from the previous P300 component that is selectively observed for an infrequent target (oddball) stimulus. Additionally, the data in the behavioural experiment showed that a time required for the detection of the RDB stimuli was longer than that of the LD stimuli by approximately 140–150 ms (Fig. 1D). This difference in the detection times suggests that the neural processing of the RDB stimuli was delayed compared to the LD stimuli by at least 100 ms in the brain. Thus, the present 300-ms component would correspond to the sensory-evoked neural activity of 100–200 ms in previous studies using the standard luminance-defined stimuli (Heinze *et al.*, 1994), rather than the N2pc component evident 250–300 ms after the stimulus onset (Hopf *et al.*, 2006). Alternatively, one possible reason for the long latency of our component was that the present 300-ms waveform reflected neural activities in a different processing stage from that in previous studies. One characteristic of our RDB stimuli is that full object identification is required to select the target, indicating a strong involvement of the higher-order visual regions. On the other hand, simple features judgement (in the lower visual areas) would be sufficient to judge the orientation of the targets defined by luminance contrast. The attentional modulation reported in the current study thus might be qualitatively distinct from that in the previous studies employing the luminance-defined stimuli.

Reorientation of spatial attention in the trial-by-trial cuing task

While we could find a significant attentional modulation in neural latency both in MEG Experiment 1 and 2, the modulation in neural amplitude was not significant in Experiment 2, which was somewhat inconsistent with several fMRI studies (Thiel *et al.*, 2004; Indovina & Macaluso, 2006). We presume this was related to the difference in the task design between Experiment 1 and 2 and the limited spatial resolution of MEG compared to fMRI. In the trial-by-trial cuing task in Experiment 2, the subjects had to answer the direction of T (upright or inverted) even in the invalid trials (although they ignored all stimuli at the unattended hemifield in Experiment 1). According to previous studies, this design would activate a reorientation network of spatial attention in the brain during the invalid trials (Corbetta *et al.*, 2000; Giessing *et al.*, 2004; Thiel *et al.*, 2004), typically producing the strong activation in the parietal areas (e.g. right temporal-parietal junction, R. TPJ) and middle frontal gyrus. A previous fMRI study further reported an enhancement of

functional connectivity during the invalid trials between the TPJ and ventral occipital cortex corresponding to the unexpected (unattended) hemifield (Indovina & Macaluso, 2004). Altogether these studies suggest that, in the invalid trials of Experiment 2, the reorientation mechanisms of the brain induced some additional activation in the higher visual regions contralateral to the invalid target. Indeed, the number of SOIs in our Experiment 2 (33.1 per subject) was slightly larger than that in Experiment 1 (27.8 per subject), suggesting that broader regions in the visual cortex were activated in Experiment 2. Although a fine spatial resolution of fMRI enabled the previous studies to focus on smaller regions where the attentional enhancement (a greater activity in the valid than invalid trials) was retained, the limited spatial resolution of MEG and our macro-level approach (grand-averaging across all SOIs) might make it difficult to distinguish these subregions, which allowed the confounding of those additional activities and produced the lack in attentional enhancement consequently.

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Abbreviations

BA, Brodmann area; ECD, equivalent current dipole; EEG, electroencephalography; EPI, echo-planar imaging; FG, fusiform gyrus; fMRI, functional magnetic resonance imaging; LD, luminance-defined; MEG, magnetoencephalography; RDB, random-dot blinking; RT, reaction time; SOI, sensor of interest; VEF, visual-evoked field.

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