Asymmetrical brain activity induced by voluntary spatial attention depends on the visual hemifield: A functional near-infrared spectroscopy study

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1. Introduction

Visuospatial attention enables the simultaneous tracking of the trajectories of multiple objects (Pylyshyn & Storm, 1988). This indicates that our visual system can divide attention and process multiple objects in parallel. Several previous studies have reported that approximately four objects can be tracked simultaneously (Interrilligator & Cavanagh, 2001; Pylyshyn & Storm, 1988; Yantis, 1992), and that the cognitive capacity of tracking—the resources for attention processing—is limited. Alvarez and Cavanagh (2005) psychologically investigated the mechanisms involved in attentional resources. Using an multiple object tracking (MOT) task, they found that the behavioral performance of observers tracking the same number of targets varied when the targets were presented in both the left and right visual hemifields and when they were presented in only one visual hemifield. Therefore, the authors concluded that independent resources must exist for attentional tracking in the left and right visual hemifields.

Several previous studies have investigated the neural substrates of the resources involved in visuospatial attention. Culham et al. (1998) conducted a human neuroimaging study using fMRI. They found that the posterior parietal cortex (PPC), including the intraparietal sulcus (IPS), was activated while maintaining voluntary attention during the MOT task. Drew and Vogel (2008) showed that the amplitude of event-related potentials measured in posterior electrode sites increased as the number of targets in the MOT task increased. Using transcranial magnetic stimulation (TMS), Battelli, Alvarez, Carlson, and Pascual-Leone (2008) showed that the behavioral performance of the MOT task declined when the observers’ IPSs were deactivated. These findings suggest that the neural substrates of the attentional resources involved in MOT are located in the PPC, which includes the IPS.

It is unclear whether or not the finding of Alvarez and Cavanagh (2005), i.e., the existence of functionally independent attentional resources for the two visual hemifields, is consistent with the findings of the abovementioned cognitive neuroscience studies. It is widely believed that the visual input from each visual hemifield is primarily processed in the contralateral cerebral hemisphere, at least in the early processing stages. Battelli et al. (2008) showed that in tracking tasks, when the target stimuli are presented in both visual hemifields, TMS of the IPS deteriorates the tracking performance for the target stimuli presented in the visual hemifield contralateral to the stimulated IPS. This implies that the attentional resources for a given visual hemifield are located in the contralateral hemisphere.

Further, neuropsychological studies have showed that lesions in the right inferior parietal lobule induce left hemispatial neglect (reviewed in Mort et al., 2003). This has led to the hypothesis that the right hemisphere is dominant in the processing of spatial attention and that it is involved in the processing of both visual hemifields (Heilman & Van Den Abell, 1980). In addition, since the dominance

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of the two hemispheres varies with different tasks (Macaluso & Frith, 2000), it is unlikely that both hemispheres are equally involved in the processing of visuospatial attention.

As mentioned above, little is known about the relationship of cerebral activity with the attentional processing of signals from each visual hemifield. In particular, it is unclear how the attentional resources required for each visual hemifield are functionally separated between the cerebral hemispheres. An in-depth analysis of this separation, we believe, yields deeper insights into the neural substrates of spatial attention.

Therefore, in this study, we measured brain activity while the visuospatial attention was oriented to a particular location in the visual field and investigated the neural representation of attentional space for both the left and right visual hemifields. For the orientation of visuospatial attention, we used visual stimuli similar to those used by Alvarez and Cavanagh (2005), and we measured brain activity by using optical topography—a non-invasive method involving near-infrared spectroscopy. Optical topography can optically measure changes in the oxy-hemoglobin (Hb), deoxy-Hb, and total-Hb concentrations in tissue by measuring changes in the absorption of near-infrared light at different wavelengths (Jobsis, 1977). Since the brain activity measured by this technique depends on the cortical metabolism, the measured brain activity lags behind the spikes of neurons by several seconds, and its temporal resolution is limited by a blurred intrinsic hemodynamic response (Kim, Richter, & Ugurbil, 1997). Therefore, optical topography is suitable for experimental tasks requiring the regulation of sustained attention (for example, an MOT task). Since the PPC has been reported to be involved in the execution of the MOT task (Culham et al., 1998), we positioned optical probes such that they covered the PPC and early visual cortex. Using the abovementioned procedure, we investigated the neural representation of voluntary visuospatial attention for both the left and right visual hemifields.

2. Methods

Participants gazed at a central fixation cross and tracked rotations of windmill-like gratings with covert attention. We varied the number and positions of the tracked gratings and measured the brain activity in the posterior cortex by using functional near-infrared spectroscopy (fNIRS).

2.1. Participants

We tested 20 healthy participants who were aged 18–46 years and had normal or corrected-to-normal vision. Prior to the experiments, each participant signed an informed consent form in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The participants received remuneration for their involvement in the experiment. All participants were trained for the experimental task in a preliminary experiment.

2.2. Apparatus

We used a 22" CRT display (Iiyama; HM204D, 1024 × 768 pixels, Vsync 100 Hz) or a 50" plasma display panel (PDP) (Panasonic; TH-50PX510, 1024 × 768 pixels, Vsync 60 Hz) and a PC for presenting the visual stimuli. We generated and controlled the visual stimuli by using MATLAB on Windows XP and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The viewing distance was 77 cm for the CRT and 140 cm for the PDP. A video-based eye-movement tracker (Takei) was used for monitoring the participants’ eye fixation. Trials in which the participants continuously gazed 2° or more away from the fixation cross for 500 ms were excluded from the analysis. Brain activity was measured using the Optical Topography system ETG-100 (Hitachi Medical Systems). All experiments were conducted in a dark room.

2.3. Visual stimuli

The stimuli were high-contrast, sinusoidal radial gratings. In each trial, a fixation cross (height and width, 1°) and four gratings (radius, 3°) were presented; each grating was centered at a corner of an imaginary square subtending 8.5° × 8.5°, such that each corner was 6° from the fixation cross. These stimuli and the tasks performed in this study were modified from those used by Alvarez and Cavanagh (2005).

2.4. Procedure

The participants were asked to track the rotation of one or two cued gratings with covert attention while gazing at the central cross. The target grating(s) (i.e., the ones that were to be tracked) were indicated by cueing stimuli—line segments of the same color as the fixation cross.

The sequence of the trials was as follows: First, a green or red fixation cross and four radial gratings were displayed. Subsequently, red or green line segments (cueing stimuli) were displayed over each radial grating and blinked three times. One or two line segments were displayed in the same color with the fixation cross, whose color varied with the experimental conditions. After blinking, the line segments disappeared, and the fixation cross turned white. After 1 s, all the gratings rotated for 10 s at a constant speed. The direction of rotation of each grating was randomly determined and reversed at random intervals (once a second on average). After the rotation ended, the white fixation cross appeared colored, and the line segments (cue stimuli) were displayed and blinked again. Using the above procedure, the participants were presented identical stimuli patterns during the rotations in all experimental conditions.

At the end of the trials, the accuracy of tracking was tested in the two-alternative forced-choice procedure. Participants reported whether or not the cued stimuli presented before and after the rotations were identical, i.e., whether the relative angular positions of the target gratings and the line segments were identical before and after the rotations. In trials in which the participants were required to track the two targets simultaneously, only one line segment was presented over a randomly selected target during the response period (Fig. 1, right). In 50% of the trials, the angular position of the line segment relative to the target stimulus was altered by ±90° from the initial relative position. After the participants had responded, the stimulus display turned uniformly gray. The intertrial interval was 15 s.

The rotation speed was adjusted for each participant on the basis of his/her performance in the preliminary trials such that his/her correct response ratio in single-target tracking trials was 90% (averaged speed, 113°/s). In dual-target tracking trials, the target stimuli were adjoined either vertically or horizontally, and these conditions were termed unilateral and bilateral conditions, respectively. Thus, eight different experimental conditions were created, depending on the number and position of targets (Fig. 2). All the conditions were repeated 6 times in a session consisting of 48 trials. The participants were rested after every 12 trials. A total of eight subjects participated in one session each, and 12 subjects participated in two sessions each.

2.5. Measurement

We used the Optical Topography system ETG-100 for measuring brain activity. This system is equipped with two types of near-infrared optical laser diodes with radiating wavelengths of 780
assessed using the 2AFC task.

The behavioral performance in the tracking task and the changes in oxy-Hb concentrations were analyzed according to the number and position of the target stimuli. The data for the unilateral and bilateral conditions were separately analyzed (Fig. 2). The unilateral condition included the Left-1, Left-2, Right-1, and Right-2 conditions, and the bilateral condition included the Upper-1, Upper-2, Lower-1, and Lower-2 conditions. The above conditions are named according to the number and position of the target stimuli; for example, “Left-1” indicates that one target stimulus was presented in the left visual hemifield. A trial in which the target grating was in the lower left visual hemifield was designated both Left-1 and Lower-1.

3. Results

Table 1 shows the correct response ratio for each experimental condition. The behavioral performance significantly differed among the three conditions (single-target, unilateral, and bilateral conditions) ($F(2, 38) = 19.43; p < .001$). Increase in the number of targets generally deteriorated the performance. This tendency was significant in the unilateral condition ($t(19) = 5.90; p < .001$), while it was not clear in the bilateral condition ($t(19) = 1.85; p = .24$). In trials involving two targets, a significant difference was observed between the unilateral and bilateral conditions ($t(19) = 3.31; p < .05$). These trends are similar to those reported by Alvarez and Cavanagh (2005).

Table 1

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3.1. Behavioral performance

Table 1 shows the correct response ratio for each experimental condition. The behavioral performance significantly differed among the three conditions (single-target, unilateral, and bilateral conditions) ($F(2, 38) = 19.43; p < .001$). Increase in the number of targets generally deteriorated the performance. This tendency was significant in the unilateral condition ($t(19) = 5.90; p < .001$), while it was not clear in the bilateral condition ($t(19) = 1.85; p = .24$). In trials involving two targets, a significant difference was observed between the unilateral and bilateral conditions ($t(19) = 3.31; p < .05$). These trends are similar to those reported by Alvarez and Cavanagh (2005).

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In the unilateral condition, the difference between Left-2 and Right-2 was not significant \( (F(1, 19) = 0.84; p = .37) \), while the difference between Lower-2 and Upper-2 in the bilateral condition was significant \( (F(1, 19) = 5.02; p < .05) \). These findings suggest the dominance of the lower visual hemifield in MOT tasks (Intriligator & Cavanagh, 2001).

For the 12 participants who participated in the two sessions, there was no clear difference of the performance between the first (79.7%) and the second (81.6%) \( (t(11) = .72, p = .49) \).

3.2. Analysis of fNIRS data

The fNIRS data from the participants whose behavioral performance was better than some criteria were mainly used for the analysis. Since in the condition with two targets the tested target was randomly selected from those two, chance level of tracking accuracy should be 75% when a participant tracked only one target successfully. The 10 participants whose averaged behavioral performance in the unilateral condition was less than 75% were hence not used for further analysis. The remaining 10 participants with the higher performance showed a significant decline in performance with an increase in the number of target stimuli in the unilateral condition \( (F(1, 19) = 4.15; p < .05 \) and \( t(19) = 3.27; p < .05 \), Table 2). No other significant differences were seen. The averaged numbers of sessions which the participants performed were 1.4 and 1.8 for the higher- and lower-performance groups, respectively.

The observed changes in the oxy-Hb concentration for each participant, measurement point, and session were band-pass filtered (passband: 0.01–1.0 Hz). Since raw data of fNIRS are relative values, we cannot directly compare them among participants or channels. Therefore, the values obtained after filtration were normalized using standard deviations of the amplitudes of the changes in oxy-Hb concentrations during the rest periods (i.e., 6 s before the presentation of the cueing stimuli, which appeared 4 s before the onset of rotation) for each channel within participants (Matsuda & Hiraki, 2006; Otsuka et al., 2007; Taya, Maehara, & Kojima, 2009). Fig. 4 shows the normalized changes in oxy-Hb levels averaged over all 24 measurement points. The difference between the changes in oxy-Hb levels in the rest periods and those in the analyzed periods (6–10 s after the onset of rotation) was used as an index of the brain activity induced by the execution of the task.

3.3. Effects of the number and position of the target stimuli

Fig. 4 shows the temporal course of brain activity averaged over all measurement points for each condition. The pattern of brain activity (changes in oxy-Hb concentration) before task onset was similar in all conditions.

Fig. 5 shows the mean brain activity (oxy-Hb concentration) measured over all measurement points during the task periods. In the unilateral condition, the activity significantly increased as the number of targets increased \( (F(1, 9) = 5.25; p < .05) \), while in the bilateral condition, no significant changes were observed \( (F(1, 9) = 0.25; p = .63) \). These trends in the arrangement of target stimuli and increase in brain activity were consistent with the trends in behavioral performance of the task (Tables 1 and 2). When the difference in the performance between the single- and dual-tracking tasks was large, the difference in the activity tended to increase further. This increase in oxy-Hb concentration varied with the visual hemifield to which attention was oriented. In the unilateral condition, the increase in the brain activity due to the increase of the targets was significantly larger when attention was oriented to the left visual hemifield (Left-1, Left-2) rather than to the right visual hemifield (Right-1, Right-2) \( (F(1, 9) = 14.28, p < .01) \).

Table 2

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<td>Averaged score</td>
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p < .01). In the bilateral condition, in contrast, there was no clear difference on the visual hemifield (F(1, 9) = 0.087, p = .77).

We assumed that the five upper and five lower measurement points for each probe holder (Fig. 2) were positioned over the parietal and occipital cortices respectively (Okamoto et al., 2004). Further, we separately averaged the activities detected by these probes (Fig. 6) for the higher-performance group. In almost all measured cortical areas, the trends in the increases in the activity due to the increase of the targets in the unilateral condition (Fig. 6, upper panel) were similar to those shown in Fig. 5. The activity in the right hemisphere tended to be larger than that in the left hemisphere for all patterns of target stimuli (unilateral, \( F(1, 9) = 3.96; p = .08 \) and bilateral, \( F(1, 9) = 3.68; p = .09 \)).

In the lower-performance group it is possible that the participants’ worse behavioral performance indicates that they gave up their task due to the difficulty of the dual-tracking task (note that the performance of <75% corresponds to tracking ability of less than one target). It should be, therefore, not adequate to discuss the relationship between the number of the target and attentional load similarly with that in the higher-performance group. The trend of the brain activities of this group seems consistent with this view. In contrast to the higher-performance group, the increase of the number of targets tended to decrease the brain activity in the unilateral condition (\( F(1, 9) = 3.64, p = .09 \), Fig. 7). No clear trend was observed in the bilateral condition.

### 4. Discussion

We measured the brain activity during a task requiring participants to maintain endogenous spatial attention toward a particular location in the visual field. We then examined the relationship between task load and brain activity.

The extent of decline in task performance with increase in the number of target stimuli was significantly related to whether the targets were positioned in one visual hemifield unilaterally or in two visual hemifields bilaterally. This finding seems consistent with the hypothesis that separate attentional resources exist for each visual hemifield (Alvarez & Cavanagh, 2005). The changes in brain activity observed in our study also seem to support this hypothesis. When the number of target stimuli per visual hemifield was one or less (unilateral condition), the task performance and brain activity did not change very much as the total number of targets increased (Fig. 5, right). In contrast, when the targets were positioned only in one visual hemifield (unilateral condition), a distinct change in the brain activity was observed with increase in the number of targets as long as the participants concentrated upon the task (Fig. 5, left). The attentional load increase in the left visual hemifield increased the brain activity greatly although the effect in the right visual hemifield does not show statistically significant effect.

#### 4.1. Difference on cortical regions

The trends in the brain activity related to the arrangement of the targets were observed for both visual hemispheres almost similarly (Fig. 6). In other words, for a given task condition, the change in brain activity was similar for both hemispheres, regardless of the visual hemifield toward which attention was oriented. A pattern of contralateral dominance between attended visual fields and cerebral hemispheres was generally not observed, here. This may suggest that attentional resources functionally separated for each visual hemifield are not separated anatomically. In the left occipital area, however, the difference between Right-1 and Right-2 looks relatively larger than that in the other areas, possibly because of the contralateral dominance. We will discuss a possible interpretation of this weak contralateral dominance below.

It is intriguing that the increase in the brain activity with the increase in attentional load varied depending on the attended visual hemifield (Fig. 5, left, unilateral). When the attention was oriented to the left visual hemifield, the brain activity clearly increased with the attentional load. In contrast, when the attention was oriented to the right visual hemifield, the increase in brain activity was quite small or did not exist. However, the behavioral performance of the experimental task did not differ between the left and right visual hemifields (Table 2). This suggests that the brain activity required for the regulation of attention varies with the attended visual hemifield. This difference in the brain activity with the visual hemifield was similar for both hemispheres (Fig. 6, upper panel).
4.2. Interactions between the hemispheres

Battelli et al. (2008) evaluated behavioral performance of participants whose IPSs were stimulated using TMS during the MOT task. The experimenters controlled which visual hemifield the target stimuli were displayed in and which IPS was inhibited using TMS. They concluded as follows: First, both hemispheres are involved in tracking objects in both visual hemifields; however, the contralateral hemisphere is dominantly involved. Second, the hemispheres interact with each other and inhibit the processing of information related to tracking in the contralateral hemisphere. Third, the interaction is asymmetrical, and the inhibition of the right hemisphere by the left is stronger than that of the left hemisphere by the right. The above findings do not contradict the findings of a previous psychophysical study (Chokron, Brickman, Wei, & Buchsbaum, 2000) that indicated that exogenous attention is left-hemisphere dominant and endogenous attention is right-hemisphere dominant. The findings of Battelli et al. (2008) also agree with those of a previous human neuroimaging study (Nobre et al., 1997) that indicated that the left PPC is more involved in the regulation of attention than the right PPC.

In this study, in the unilateral condition, increase in the attentional load in the left visual hemifield induced a larger change in the activities of both hemispheres than that induced by increase in the attentional load in the right visual hemifield. This result might be accounted for by the asymmetrical interhemispheric inhibitory interaction as follows (Fig. 8): When targets are presented in the left visual hemifield, processing of tracking occurs primarily in the right hemisphere. Since the right hemisphere only weakly inhibits the left hemisphere in response to an increase in the attentional load, processing in the left hemisphere is less inhibited. Therefore, the increase of the summed brain activities of both hemispheres would be larger (Fig. 8, left). On the other hand, when targets are presented in the right hemifield, processing of tracking primarily occurs in the left hemisphere. Since the left hemisphere strongly inhibits the right hemisphere in response to an increase in the attentional load, the activity of the right hemisphere is considerably suppressed, and therefore, the total increase in the activities of both hemispheres would be smaller (Fig. 8, right). Thus, since the increasing attentional load induced asymmetrical inhibitory interactions between the hemispheres, the increase in the whole-brain activity is also asymmetrical, and this activity varies with the attended visual hemifield. The asymmetry was observed depending on the visual field, and an increase in the brain activity was observed similarly in all cortical regions examined in both hemispheres. This suggests that the inhibition induced in both hemispheres was diffusely and extensively distributed over the cortical areas, mainly the occipital and parietal areas, via both afferent and efferent networks. According to this hypothetical model, the lack of the difference of the brain activity related to the elevation of the attentional load in the right hemifield would be possibly due to the greater inhibitory interaction from the left to the right hemisphere.

Our brain activity data does not necessarily support the model definitively, since we could not measure the brain activity related to the intermediate processes in the model (Fig. 8, Hypothetical activities). That might be possibly because of the technical limitation of fNIRS which could not directly measure the brain activity in the sulci or in other deeper cortical regions including IPS. With this assumption, however, the model can be a likely candidate for a hypothesis giving an account of our data.

The visual hemifield-dependent asymmetric brain activity observed in this study, at least partially, supports the hypothesis that asymmetrical inhibitory interactions exist between the...
hemispheres and suggests that such inhibitory signals can diffuse across very wide cortical areas. To support this model further, it is necessary to acquire the brain activity data related to the intermediate process of it and to the propagation process of the interhemispheric inhibitory interaction.

5. Conclusions

In this study, we investigated the relationship between the brain activity during the continuous regulation of endogenous visuospatial attention and the location toward which the spatial attention was oriented. The observed changes in brain activity seemed to be consistent with the findings of a previous psychophysical study that reported the functional separation of attentional resources between visual hemifields. The change in brain activity induced by an increase in attentional load was clearly larger in the case of the left visual hemifield than in the case of the right visual hemifield. This trend seems to be accounted for by the asymmetry of inhibitory interactions between the hemispheres. In addition, this finding of asymmetrical brain activity was observed in very wide cortical areas, suggesting that inhibitory signals originating in the PPC, including the IPS, are extensively diffused via both afferent and efferent networks.

References
