Differential Contributions of the Intraparietal Sulcus and the Inferior Parietal Lobe to Attentional Blink: Evidence from Transcranial Magnetic Stimulation

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Abstract

■ When two targets (T1 and T2) are to be identified in rapid serial visual presentation, the response to T1 induces impairment of T2 report if T2 appears within 500 msec after T1 (attentional blink: AB). AB is thought to reflect temporal limitations of attention which affect target perception. Recent research suggests that the intraparietal sulcus (IPS) contributes to an attentional set associated with task goals, whereas the inferior parietal lobe (IPL) is associated with the disengagement and reorienting of attention to a relevant stimulus presented outside the current focus of attention. We investigated respective involvement of the IPS and the IPL in AB using transcranial magnetic stimulation (TMS). The results of Experiment 1 showed that the magnitude of AB deficit decreased TMS disrupted activity of the IPS after T1 onset. In addition, an increased AB deficit occurred when TMS was delivered over the IPS or IPL after T2 onset. In Experiment 2, where participants were instructed to ignore T1, they showed an AB-like T2 deficit only when TMS was delivered to the IPS after a T2 onset. Findings are discussed in terms of hypotheses about the respective roles of the IPS, in realizing an attentional set, and the IPL, in contributing to a disengagement of attention (from T1 to T2) during an AB period. ■

INTRODUCTION

Often, when events are rapidly presented, we fail to perceive them accurately due to temporal limits placed on attention. In laboratory studies, this phenomenon has been demonstrated using the rapid serial visual presentation (RSVP) paradigm, in which visual items are presented sequentially at a given spatial location, each for a very brief duration (i.e., between 50 and 120 msec). Typically, these sequences include two targets, denoted T1 and T2, where T2 follows T1 within a series of distractors. When asked to attend to both targets, people often fail to identify T2 if it follows T1 too closely in time. That is, if the SOA between T1 and T2 is between 200 and 500 msec, attending to T1 interferes with T2 processing (Raymond, Shapiro, & Arnell, 1992). This interference is referred to as the attentional blink (AB). The duration of an AB has generally been assumed to reflect a period during which attention is fully engaged in T1 processing, disrupting reorienting to T2 (Shapiro, Arnell, & Raymond, 1997).

The present research examines whether different brain regions are implicated in the attentional demands associated with detecting the two targets within the AB task. fMRI studies have shown that fronto-parietal regions are more strongly activated in participants who exhibit a weak AB than for those who exhibit a robust AB (Feinstein, Stein,

Castillo, & Paulus, 2004). Electroencephalography (Sergent, Baillet, & Dehaene, 2005) and magnetoencephalography (Gross et al., 2004) studies also point to a cortical network involving frontal, parietal, and occipital cortex that is engaged during an AB task. Successful T2 report has been associated with activation of fronto-parietal (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005) or parieto-occipital cortices (Hein, Alink, Kleinschmidt, & Müller, 2009). Posterior parietal region is activated during an AB task, but these activations were independent of the occurrence of a T2 report. In contrast, activations in frontal and medial temporal cortices were associated with a T2 report (Marois, Yi, & Chun, 2004).

The present study focuses on the role of posterior parietal cortex in AB. This region is critical for the allocation of visual attention (e.g., Wojciulik & Kanwisher, 1999; Coull & Nobre, 1998). Two subregions within posterior parietal cortex, the intraparietal sulcus (IPS) and the inferior parietal lobule (IPL), have been related to AB (for a review, see Marois & Ivanoff, 2005). For example, the IPS is activated when participants identify T1 (Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois, Chun, & Gore, 2000). This is further supported by evidence showing that performance on the AB task can be influenced by TMS over parietal cortex. Cooper, Humphreys, Hulleman, Praamstra, and Georgeson (2004) showed that the magnitude of an AB deficit for T2 was significantly *reduced* when 8-Hz triple-pulse TMS was applied to right posterior parietal

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cortex. Kihara et al. (2007) reported a similar result using single-pulse TMS delivered to the IPS 350 msec after T1 onset. The attenuation of the AB effect could be due to the fact that TMS facilitated attentional disengagement from T1 to T2. These findings suggest that the IPS is critically involved in T1 processing in the AB paradigm.

Other subregions of posterior parietal cortex appear to be more relevant to T2 processing. Specifically, the IPL, including the temporo-parietal junction, has been linked to attentional processes related to the onset of T2 in the AB task. fMRI studies have shown that the IPL was activated more strongly when T2 was correctly reported compared to when T2 was missed (Hein et al., 2009; Shapiro, Johnston, Vogels, Zaman, & Roberts, 2007; Kranczioch et al., 2005). Lesion studies in humans also support IPL involvement in T2 processing. Husain, Shapiro, Martin, and Kennard (1997) reported that recovery from an AB deficit following T1 (i.e., the effective SOA associated with correct T2 reports) took longer in patients with right parietal damage. A follow-up study indicated that damage to the IPL, rather than to the superior parietal lobule, caused this protracted AB (Shapiro, Hillstrom, & Husain, 2002). These results suggest that the IPL is responsible for successful detection or identification of a T2 when presented within the AB period.

Although previous research indicates a relationship between the IPS, the IPL, and AB, the functional contribution of these two neural regions to AB remains unclear. Studies using the Posner (1980) cuing task suggest that the IPS and the IPL make distinct contribution to visual attention. For example, Corbetta, Kincade, Ollinger, McAvoy, and Shulman (2000) found bilateral IPS activation when attention was maintained at a cued location, whereas the right IPL was activated when the target appeared in a different location from the cue. Corbetta et al. proposed that the IPS is involved with attentional set, namely, the focusing of attention on current behavioral goals. In contrast, the IPL is associated with disengagement of focal attention from its current focus and reorienting it to relevant stimuli. The attentional contributions of the IPS and the IPL are not confined to the spatial domain. The IPS is activated by non-spatial cues which direct focal attention to a specific target feature, such as color or shape (Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007; Rushworth, Paus, & Sipila, 2001; Le, Pardo, & Hu, 1998) or time point of target onset (Coull, Frith, Büchel, & Nobre, 2000). Similarly, the IPL is activated if focal attention is reoriented from a time point indicated by an invalid cue to the actual target onset (Coull et al., 2000).

The present study uses TMS to compare the role of the IPS and the IPL in the AB task. In this task, observers must establish an attentional set to report both T1 and T2 (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Isaak, Shapiro, & Martin, 1999; Ross & Jolicœur, 1999; Maki, Couture, Frigen, & Lien, 1997). We offer two hypotheses. The *attentional set hypothesis* focuses on the role of the IPS in focal attending to any target embedded in a RSVP

(Kihara et al., 2007; Cooper et al., 2004; Marcantoni et al., 2003; Marois, Chun, et al., 2000). When TMS disrupts IPS activity during T1 processing, participants should be faster in disengaging attention from T1 to T2; that is, participants should be better at responding to T2 (Kihara et al., 2007). However, when TMS is delivered to the IPS after T2 onset, orienting to T2 should be disrupted, leading to an increase in AB.

The second hypothesis, the *disengagement hypothesis*, concerns the contribution of the IPL for identification of a target appearing within the AB period. The failure of the disengagement of focal attention from T1 to T2 is one of the major causes of AB (Chua, 2005; Nieuwenstein, Chun, van der Lubbe, & Hooge, 2005; Shapiro et al., 1997). Given the role of the IPL is the disengagement and reorienting of attention (Corbetta, Patel, & Shulman, 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002), the IPL should be especially critical for disengaging attention from T1 to T2 when attention has been initially focused upon T1. Thus, we expect to find a greater AB effect when TMS is delivered to the IPL after T2 onset. Moreover, TMS delivered to the IPL after T1 onset may not affect the size of the AB deficit because disengagement and reorienting of attention does not occur before T2 onset. To investigate both of these hypotheses, we tested whether TMS delivered over either the IPS or the IPL, and after either T1 or T2, affected AB.

EXPERIMENT 1

Methods

Participants

Eleven participants were recruited. They ranged in age from 22 to 32 years old (mean = 25.5 years). Ten men and one woman participated. All were right-handed and reported normal or corrected-to-normal vision. None reported a history of neurological or psychiatric illness. The experiment was conducted in accordance with the ethical guidelines of the World Medical Association's Declaration of Helsinki and approved by the Committee of Medical Ethics, Graduate School of Medicine, Kyoto University. All participants gave written informed consent.

TMS Protocol

TMS pulses were applied using a Magstim Super Rapid Magnetic Stimulator (Magstim Co., Whitland, Dyfed, UK), equipped with an air-cooled 70-mm figure-of-eight-shaped coil (maximum output: 2.2 Tesla). Stimulation intensity was set to 60% of maximum output.

Previous studies have not revealed a consistent relationship between attention to visual events and activity in left posterior parietal cortex, especially in the IPL (Husain & Nachev, 2007). Therefore, TMS was only applied to right posterior parietal cortex, targeting the middle IPS or right IPL (Figure 1A). The IPS site was adjacent to the dorsal

border of the angular and supramarginal gyrus. The IPL site was located at the intersection of the posterior end of the superior temporal gyrus and the supramarginal gyrus (i.e., the dorsal temporo-parietal junction; cf. Corbetta & Shulman, 2002).

The targeted regions were identified from anatomical magnetic resonance images obtained for each participant prior to the experiment. Optimal coil placement was guided via a frameless stereotactic system (Brainsight; Rogue Research Inc., Montreal, Quebec, Canada). The average IPS position was 8.2 cm dorsal and 5.5 cm lateral from the inion. The average IPL position was 6.4 cm dorsal and 13.5 cm lateral from the inion. The average distance between the IPS and the IPL was 7.4 cm. To control for nonspecific TMS effects, real and sham stimulations (Robertson,

Théoret, & Pascual-Leone, 2003) were also delivered to the electrode site Cz. Sham TMS was carried out using a specially designed sham coil that induced no magnetic field but produced a similar auditory noise. During the TMS experiment, the TMS coil was held by an articulated arm clamp that allowed for fixation of the coil on the target position, with the handle of the coil pointing backward. Event-related triple-pulse TMS was delivered at a frequency of 13.3 Hz (i.e., 75, 150, and 225 msec after T1 or T2 onset).

AB Task

Participants were seated in a dimly illuminated, electrically shielded room. The RSVP items were presented on a 17-in. color CRT monitor with a 100-Hz refresh rate driven by

Figure 1. (A) Single-participant example of the TMS locations. Left: White cross indicates the area identified as the IPS. Right: White cross indicates the area identified as the IPL. (B) Schematic illustration of experimental procedures in the 300-msec T1–T2 SOA condition. (C) Schematic illustration of experimental procedures in the 800-msec T1–T2 SOA condition. Each RSVP item was presented for 50 msec with an interstimulus interval of 0 msec. Triple-pulse TMS was delivered at 75, 150 and 225 msec after T1 or T2 onset. *TMS after T1* is the condition in which TMS was delivered after T1 onset. *TMS after T2* is the condition in which TMS was delivered after T2 onset. The white cross was the fixation stimulus presented for 1000 msec. The digits were targets and the letters were distractors. *T1* is the first target. *T2* is the second target.

Presentation software (Neurobehavioral Systems, Albany, CA). The viewing distance was 57 cm and the RSVP items subtended about 1° × 1° of visual angle. Each RSVP sequence comprises two digits (targets) and several letters (distractors). For a given sequence, targets were randomly selected from digits 1 to 9, with the constraint that T1, the first target, differs from T2, the second target. Distractors were selected from uppercase letters (A–Y, excluding B, I, O, and Q); no letter appears successively within a sequence. Each RSVP item was presented for 50 msec with no interval between items. The luminance of the RSVP items was adjusted for each participant (see below), and the screen background luminance was 0.39 cd/m².

Each trial began with a 1000-msec display of a fixation cross at the center of the screen followed by the RSVP stream. T1 appeared 400–800 msec after the RSVP started. T2 appeared within (i.e., 300 msec after T1 onset) or outside (i.e., 800 msec after T1 onset) the presumed AB period. These values were selected given that the typical AB period is between 200 and 500 msec (Shapiro et al., 1997). After the stimulus stream, participants entered their responses. Participants were instructed to sequentially report T1 and T2 by pressing the appropriate key at their own speed during the response phase. Participants were encouraged to guess if they were uncertain. No feedback about performance was provided. Following the response phase, the screen was blank for an intertrial interval of 6000 msec.

Procedure

Figure 1B and C shows the experimental procedures. Given that there are individual differences in the magnitude of AB (e.g., Martens, Munneke, Smid, & Johnson, 2006; Feinstein et al., 2004), we conducted a preliminary experiment without TMS to determine optimal conditions for a stable magnitude of AB in each participant. Using the method of limits, the critical luminance of the RSVP items was established individually for each participant (cf. Christmann & Leuthold, 2004). The luminance values for the RSVP items ranged from 1.6 to 70.4 cd/m² across participants (mean luminance = 42.1 cd/m²).

Participants completed four sessions, where each session consisted of four blocks. The position of the stimulator was varied across blocks (right IPS, right IPL, Cz, and sham). The order of stimulation sites was counterbalanced across sessions. Each block consisted of 40 trials. TMS pulses were applied at one of two timings (after T1 onset condition and after T2 onset condition) and two T1–T2 SOAs (300-msec condition and 800-msec condition). Each of these four conditions was repeated 10 times in a block. A total of 640 trials were given to each participant (4 Stimulation sites × 2 Timings of TMS × two T1–T2 SOAs × 10 trials × 4 sessions). Each session was preceded by a practice block of 40 trials and took about 30 min, and each of these sessions was conducted after an interval of at least 30 min.

Results

Trials in which the items were reported in reverse order were scored as correct. The results are shown in Figure 2. In terms of T1, a three-way repeated measures analysis of variance (ANOVA) did not yield any significant main effects or interactions (all $ps > .05$). A similar analysis of T2 performance was restricted to trials in which T1 was correctly reported. In this analysis, the main effect of T1–T2 SOA was significant [$F(1, 10) = 121.8, p < .01$], demonstrating that we obtained a robust AB effect.

The ANOVA also yielded significant interactions between the timing of TMS and T1–T2 SOA [$F(1, 10) = 6.94, p < .05$], and the timing of TMS, T1–T2 SOA and TMS site [$F(3, 30) = 8.73, p < .01$]. Post hoc t tests indicated that T2 performance in the 300-msec T1–T2 SOA condition was poorer than performance in the 800-msec T1–T2 SOA conditions under each condition (all $p < .01$), except under IPS TMS after T1 condition [$t(10) = 1.18, p > .26$]. These results suggest that triple-pulse TMS attenuated the AB effect when TMS was delivered to the IPS after T1 onset.

Because of the significant three-way interaction, we conducted analyses of the magnitude of T2 deficit by subtracting T2 performance in the 300-msec T1–T2 SOA condition from the 800-msec condition (Giesbrecht, Sya, & Lewis, 2009; Jackson & Raymond, 2006). In the TMS after T1 onset condition, there was a significant effect of TMS site [$F(3, 30) = 3.98, p < .02$; Figure 2C]. The magnitude of T2 deficit was smaller for the IPS condition compared to the IPL, Cz, and sham conditions [$t(10) = 2.61, p < .03$; $t(10) = 2.33, p < .05$; and $t(10) = 2.42, p < .04$, respectively]. No significant differences were found between IPL and Cz conditions [$t(10) = 0.81, p > .43$], between IPL and sham conditions [$t(10) = 0.68, p > .51$], and between Cz and sham conditions [$t(10) = 0.28, p > .78$]. These findings suggest that triple-pulse TMS decreased AB when it was delivered over the IPS after T1 onset.

Subsequent tests evaluating the effects of TMS after T2 onset condition yielded a significant effect of TMS site [$F(3, 30) = 4.67, p < .01$; Figure 2F]. The magnitude of the T2 deficit was larger under the IPS condition than under the Cz and sham conditions [$t(10) = 2.35, p < .03$ and $t(10) = 2.31, p < .05$, respectively]. The magnitude of the T2 deficit was also larger under the IPL condition than under Cz and sham conditions [$t(10) = 2.85, p < .02$ and $t(10) = 2.84, p < .02$, respectively]. However, there were no significant differences between IPS and IPL conditions [$t(10) = 0.30, p > .76$], and between Cz and sham conditions [$t(10) = 0.70, p > .50$]. These findings indicated that AB was increased by triple-pulse TMS applied over the IPS or the IPL after T2 onset.[1]

Discussion

The results of Experiment 1 demonstrate that TMS delivered over the IPS after T1 onset attenuated AB, whereas

Figure 2. Results of Experiment 1. (A) Mean correct report of T1 as a function of T1–T2 SOA in TMS after T1 onset condition. (B) Mean correct report of T2 given correct report of T1 as a function of T1–T2 SOA in TMS after T1 onset condition. (C) Mean magnitude of T2 deficit given by subtracting T2 performance under the 300-msec condition from that under the 800-msec condition in TMS after T1 onset condition. (D) Mean correct report of T1 as a function of T1–T2 SOA in TMS after T2 onset condition. (E) Mean correct report of T2 given correct report of T1 as a function of T1–T2 SOA in TMS after T2 onset condition. (F) Mean magnitude of T2 deficit given by subtracting T2 performance under the 300-msec condition from that under the 800-msec condition in TMS after T2 onset condition. *IPS* is the condition in which TMS was delivered over the IPS. *IPL* is the condition in which TMS was delivered over the IPL. *Cz* is the condition in which TMS was delivered over Cz. *sham* is the condition in which sham TMS was delivered over Cz. Error bars indicate standard errors of the mean. Significant ($p < .05$) differences are marked with an asterisk.
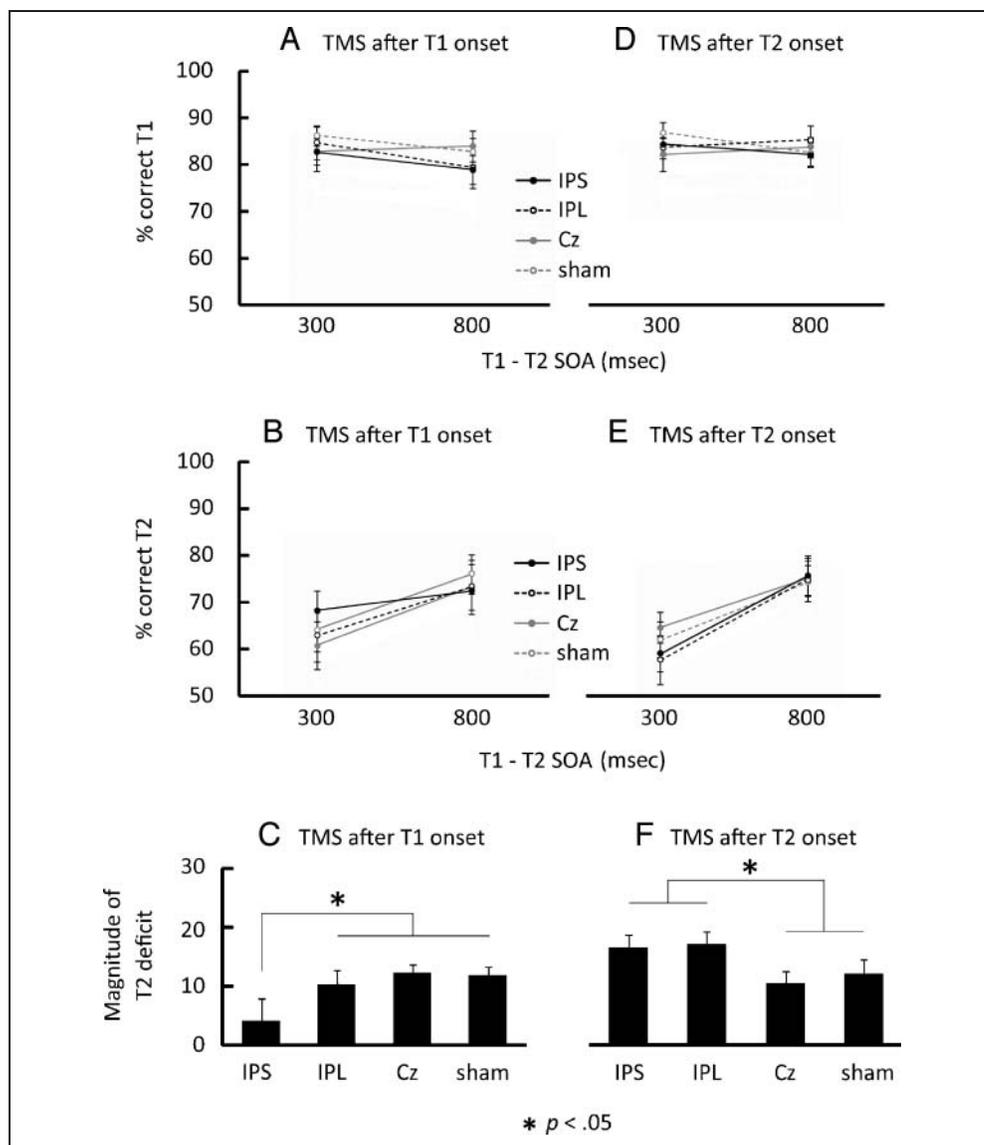
TMS delivered to the IPS after T2 onset increased AB. These results are consistent with the attentional set hypothesis, which holds that the IPS generates and/or maintains an attentional set (Corbetta et al., 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002). Within the framework of the AB task, this set maintenance would be required for both RSVP targets. The attenuation of the AB effect after T1 suggests that TMS facilitates attentional disengagement from T1, allowing the participant to orient more rapidly to T2 (Kihara et al., 2007). Similarly, the increased AB when TMS is applied to the IPS after T2 could be due to the disruption of the attentional set for a T2 that appears within the AB period.

Our results also showed that TMS over the IPL increased AB when applied after T2 onset, but not when applied after T1 onset. These findings suggest that the IPL is involved in T2 processing, but not in T1 processing. Because reorienting of attention to T2 following disengagement from T1 would be critical for the successful report of T2 (Chua,

2005; Nieuwenstein et al., 2005; Shapiro et al., 1997), this pattern is consistent with the disengagement hypothesis (Corbetta et al., 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002), required for the report of T2 within the AB period.

EXPERIMENT 2

In the next experiment, we further examined the role of the IPS in RSVP reports. Because Experiment 1 showed that AB was increased by TMS after T2 to both the IPS and the IPL, it is difficult to clearly distinguish whether this effect was due to an interruption of an attentional set for T2 or an impaired disengagement and reorienting of attention from T1 to T2. To address this issue, we included a condition in which participants were instructed to ignore T1. In this condition, a weak AB for T2 is observed (Shapiro et al., 1997; Raymond et al., 1992), presumably because the report of T2 does not require reorienting attention from

T1 to T2; rather, the attentional set for T2 must be maintained. If the IPS is associated with maintenance of attentional set, T2 performance should be disrupted in the T1-ignore condition when TMS is applied to the IPS following T2 onset compared to when TMS is applied to the IPL.

Methods

The method was the same as that of Experiment 1, except as specified below.

Participants

Twelve participants were recruited. Eight of them had participated in Experiment 1. They ranged in age from 20 to 33 years old (mean = 25.8 years). Eight participants were men and four were women.

TMS Protocol

Triple-pulse TMS was delivered over the right IPS or the right IPL. We did not include stimulation of the Cz site, using only the sham TMS control. For the sham condition, the stimulator was placed over the IPS. The average IPS position was 7.7 cm dorsal and 5.6 cm lateral from the inion. The average IPL position was 5.8 cm dorsal and 12.3 cm lateral from the inion. The average distance between the IPS and the IPL was 6.9 cm. Event-related triple-pulse TMS was delivered only after T2 onset.

AB Task

Two AB-task conditions were: a standard dual-report condition and a T1-ignore condition. In the dual-report condition, participants were instructed to identify both T1 and T2. These instructions were identical to those of Experiment 1. In the T1-ignore condition, participants were told to ignore T1 and to identify only T2.

Procedure

Luminance of RSVP items, determined in a preliminary experiment, ranged from 1.55 to 70.4 cd/m^2 across participants (mean luminance = 33.6 cd/m^2).

A previous AB study indicated that it is difficult to ignore T1 when participants had previously performed a dual-report block (Thompson, Underwood, & Crundall, 2007). Given this, the order of AB-task conditions was fixed for all participants. Participants first completed the T1-ignore condition and then the dual-report condition. The TMS session consisted of right IPS, right IPL, and sham TMS blocks in each AB-task condition. A total of 480 trials was given to each participant (2 AB-task conditions × 3 Stimulation sites × 2 T1–T2 SOAs × 40 Trials).

Results

T1-ignore Condition

Figure 3 presents the results for Experiment 2. A two-way repeated measures ANOVA revealed a significant main effect of TMS site [$F(2, 22) = 3.71, p < .05$], a main effect of T1–T2 SOA [$F(1, 11) = 8.37, p < .02$], and an interaction between the T1–T2 SOA and TMS site [$F(2, 22) = 4.34, p < .03$]. There was a significant difference between the 300-msec condition and the 800-msec condition in the IPS condition [$t(11) = 3.50, p < .01$], but not in the IPL and sham conditions [$t(11) = 1.85, p > .09$ and $t(11) = 1.11, p > .29$, respectively]. Subsequent analyses of the magnitude of T2 deficit (Figure 3B) revealed significant differences between the IPS and IPL conditions [$t(11) = 2.22, p < .05$] and between the IPS and sham conditions [$t(11) = 2.59, p < .03$], but not between the IPL and sham conditions [$t(11) = 0.27, p > .79$]. These findings suggest that an AB-like T2 deficit is produced by IPS TMS after T2 onset even when participants ignore T1, but this deficit is not observed following TMS of the IPL.

Dual-report Condition

Trials in which the items were reported in reverse order were scored as correct. In terms of T1, a two-way repeated measures ANOVA failed to yield any significant main effects or interactions (all $p > .05$). A similar analysis of T2 performance was restricted to trials in which T1 was correctly reported. In this analysis, the main effect of T1–T2 SOA [$F(1, 11) = 21.61, p < .01$], and an interaction between T1–T2 SOA and TMS site [$F(2, 22) = 4.20, p < .03$], were significant. T2 performance in the 300-msec T1–T2 SOA condition was lower than in the 800-msec T1–T2 SOA condition under each TMS site condition [IPS condition, $t(11) = 5.66, p < .01$; IPL condition, $t(11) = 4.39, p < .01$; sham condition, $t(11) < 2.97, p < .02$]. Together, this pattern indicates that a significant AB effect occurred under all TMS-site conditions when participants were required to focally attend to both T1 and T2. Subsequent analyses of the magnitude of T2 deficit (Figure 3E) showed that there were significant differences between IPS and sham conditions [$t(11) = 2.36, p < .04$], and between IPL and sham conditions [$t(11) = 3.16, p < .01$]. No significant differences were found between IPS and IPL conditions [$t(11) = 0.10, p > .92$]. These findings replicated those of Experiment 1, indicating that the AB deficit was increased by triple-pulse TMS applied over IPS or IPL after T2 onset.

Discussion

The results of Experiment 2 suggest that the contribution of the IPS to the T2 report was clearly different from the IPL. TMS applied to the IPS after T2 onset created a deterioration in response accuracy to T2 in the T1-ignore condition; TMS to the IPL did not affect T2 accuracy. Maintenance of attentional set to identify T2 should be important

Figure 3. Results of Experiment 2. (A) Mean correct report of T2 as a function of T1–T2 SOA in T1-ignore condition. (B) Mean magnitude of T2 deficit given by subtracting T2 performance under the 300-msec condition from that under the 800-msec condition in the T1-ignore condition. (C) Mean correct report of T1 as a function of T1–T2 SOA in the dual-report condition. (D) Mean correct report of T2 given correct report of T1 as a function of T1–T2 SOA in the dual-report condition. (E) Mean magnitude of T2 deficit given by subtracting T2 performance under the 300-msec condition from that under the 800-msec condition in the dual-report condition. *IPS* is the condition in which TMS was delivered over the IPS. *IPL* is the condition in which TMS was delivered over the IPL. *sham* is the condition in which sham TMS was delivered over the IPS. Error bars indicate standard errors of the mean. Significant ($p < .05$) differences are marked with an asterisk.
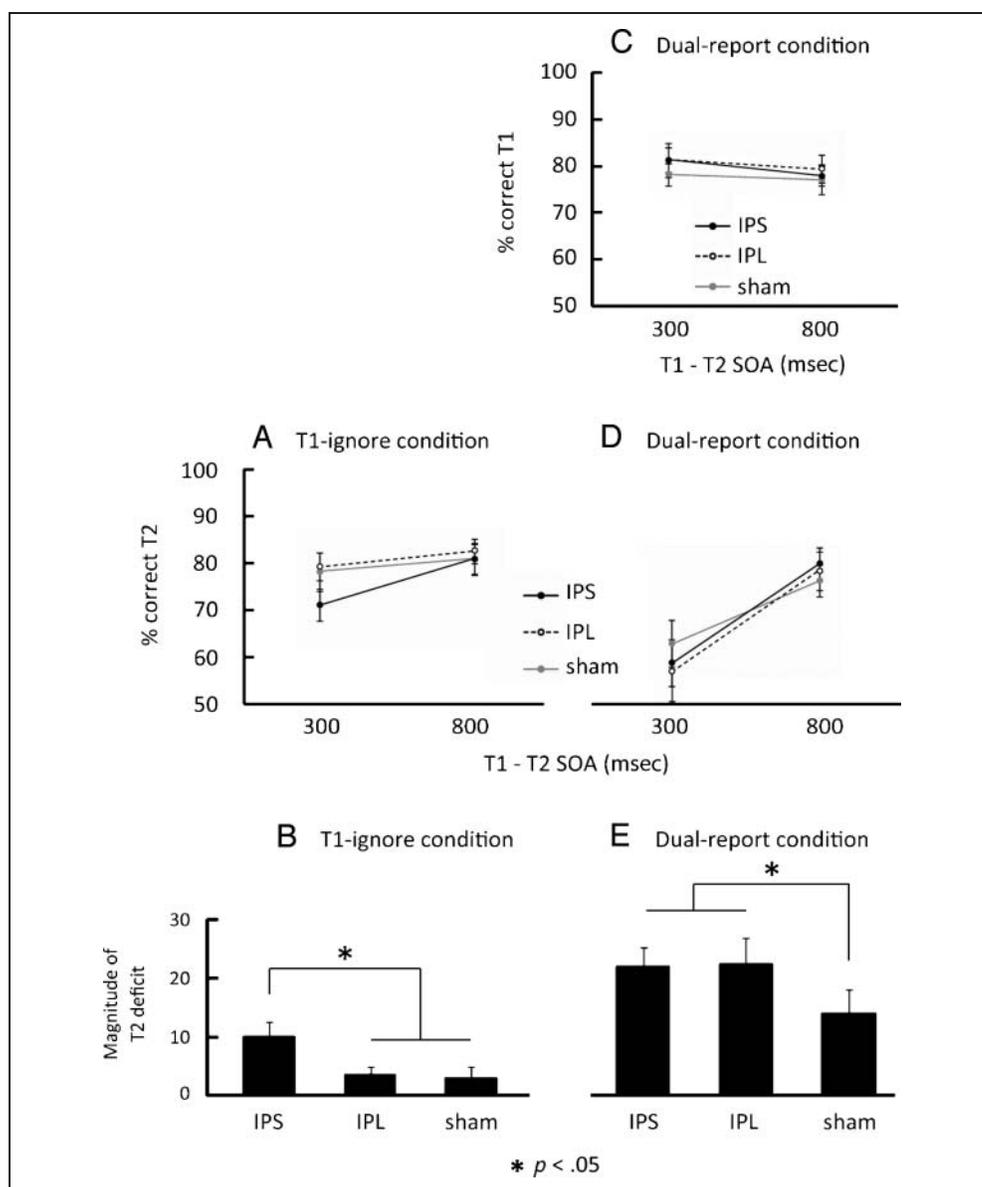
irrespective of the requirement of T1 processing. The results of IPS stimulation are consistent with the attentional set hypothesis, in which it is assumed that the IPS would be associated with the maintenance of an attentional set. This hypothesis is also consistent with previous fMRI studies demonstrating that the IPS is activated when only T1 is embedded within RSVP items, suggesting that the IPS activation is required to focus on the target (Marois, Chun, et al., 2000; Wojciulik & Kanwisher, 1999).

The results for IPL stimulation are compatible with the disengagement hypothesis in which the IPL contributes to the disengagement and reorienting of attention. In the T1-ignore condition, engaging attention to T1 is not necessary. Attentional disengagement from T1 to T2, essential in the dual-report condition, is not required in the T1-ignore condition. Based on this account, TMS to the IPL after T2 onset should not affect the accuracy of T2 report. When participants were asked to report both T1 and T2 (i.e., in

the dual-report condition), the delivery of TMS to either the IPS or the IPL after T2 onset increased the magnitude of an AB relative to the sham stimulation.

GENERAL DISCUSSION

This article investigated the way in which attentional mechanisms in the IPS and the IPL contribute to perception of visual events in rapid visual sequences. Previous studies have suggested that the IPS and the IPL play important roles in AB (cf. Marois & Ivanoff, 2005) and that these two brain regions may make respectively different contributions to visual attention (Corbetta et al., 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002). However, to date, the specific contributions of these regions to performance in the AB task have not been identified. Using TMS, we found that the IPS is related to a general attentional set for RSVP targets and that IPL activity is

involved in the disengagement of attention from T1 and reorienting to T2 during the AB period.

The Contribution of the IPS in AB

The present study support the idea that the IPS contributes to the attentional set in selecting task-relevant targets (Corbetta et al., 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002). Support for the attentional set was found in Experiment 1 by the divergent pattern of AB modulation when TMS was applied over the IPS. Specifically, if TMS was applied to the IPS after a T1 onset, the AB effect was attenuated, whereas applying TMS after a T2 onset caused an increase in AB magnitude. These findings suggest that the IPS is involved in processing T2. In addition, the results of Experiment 2 demonstrated that TMS delivered to the IPS after T2 onset induced an AB-like T2 deficit. Moreover, this was evident even when participants ignored T1. These findings can be explained by assuming that IPS TMS after T1 onset disrupted attentional engagement for T1 processing, thus allowing participants to prepare for T2 (Kihara et al., 2007). When IPS TMS was applied after T2 onset, this set would be disrupted and impair T2 report. In sum, we conclude that the IPS contribution to the attentional set is involved in the processing of both RSVP targets.

Several studies suggest that a temporary loss of control over the attentional set is a major factor in the failure of T2 report (e.g., Kawahara, Enns, & Di Lollo, 2006). In fact, the AB deficit is reduced when attentional set for T2 is reconfigured by a preceding stimulus that shares features with T2 (Nieuwenstein, 2006; Nieuwenstein et al., 2005). Past AB studies have suggested that backward masking of T2 (i.e., from distractors following T2) is one factor causing AB (Brehaut, Enns, & Di Lollo, 1999; Giesbrecht & Di Lollo, 1998). This might explain why TMS applied to the IPS after T2 onset created a deterioration in response accuracy for T2 in the present study. Such an application would lead to an impairment of a subject's attentional set for T2 processing, including potentially a failure to ignore subsequent distractors, resulting in an increase in backward masking of T2.

Experiments 1 and 2 appear to provide contradictory results regarding the effect of IPS stimulation after T1. The results of Experiment 1 did not show any TMS effect on T1 performance when TMS was delivered over the IPS after T1 onset (see also, Kihara et al., 2007; Cooper et al., 2004). However, the results of Experiment 2 showed that IPS TMS after T2 onset attenuated T2 performance when subjects had to ignore T1. Several studies suggested that excessive attention is devoted to T1 processing (Arend, Johnston, & Shapiro, 2006; Olivers & Nieuwenhuis, 2005, 2006; Shapiro, Schmitz, Martens, Hommel, & Schnitzler, 2006). In addition, it is well known that T1 performance tends to reach a ceiling level (e.g., Chun & Potter, 1995). In this case, TMS may not be sufficiently sensitive to detect disruptive effects on T1 accuracy. However, if T1 is

ignored, then the processing load on T2 following T1 may be increased, given the instructions to ignore T1 (Perry & Hodges, 2003). It is possible that this relatively high load allows IPS TMS after T2 onset to interfere with T2 identification in the T1-ignore task. Further research is needed to investigate whether the active ignoring of a preceding target would increase the processing load of a following target.

The Contribution of the IPL in AB

Experiments 1 and 2 indicated that delivery of TMS to the IPL after T2 onset increased the AB effect when participants identified both T1 and T2 but did not produce an AB-like T2 deficit when participants ignored T1. The disengagement and reorienting of attention from T1 to T2 is necessary under the dual-report condition, but not in the T1-ignore condition, whereas attentional set for relevant target(s) is required under both conditions.

The results of the present study indicate that the presence or absence of AB, at least partly, depends on the IPL. In general, the results support the hypothesis that the IPL contributes to attentional disengagement and reorienting (Corbetta et al., 2008; Husain & Nachev, 2007; Husain & Rorden, 2003; Corbetta & Shulman, 2002). Previous fMRI studies have shown that the IPL is more strongly activated when T2 is correctly reported than when it is not (Hein et al., 2009; Shapiro et al., 2007; Kranzcioch et al., 2005). Furthermore, other AB studies have implied that attentional disengagement from T1 to T2 is required for the correct report of a T2 that appears within the AB period (Chua, 2005; Nieuwenstein et al., 2005; Shapiro et al., 1997). The insignificant effect of IPL TMS after T1 onset in Experiment 1 can be understood in terms of IPL contribution to attentional disengagement and reorienting because these processes are not necessary before T2 onset under the dual-report condition.

The Relationship between the IPS, the IPL, and Other Regions in AB

We do not claim that the IPS and the IPL independently contribute to attentional processing of a target presented outside the current focus of attention. Instead, we have hypothesized that each region is specially implicated in certain attentional activities (i.e., attentional set vs. disengagement of attention). It is clear, however, that these activities cannot be entirely independent: Disengagement depends upon the presence of attentional engagement. Thus, it is likely that closer cooperation between the IPS and the IPL enable the disengagement of attention (Giessing, Thiel, Rösler, & Fink, 2006; Marois, Leung, & Gore, 2000). There are two possible accounts for the role of the IPL in such a cooperative action. One is that the IPL might send a disengagement signal to the IPS when a relevant stimulus is presented outside the focal attention (Corbetta et al., 2008; Corbetta & Shulman, 2002). The other is that the IPL might

modulate attentional resources to deal with increased task demands. Although both theories are consistent with the results of the present study, the latter seems unlikely because IPL activation does not correlate with task demands (Todd, Fougnie, & Marois, 2005; Shulman et al., 2003).

It has been proposed that a dorsal network including the IPS and the frontal eye field prevents IPL activity, suppressing attention to irrelevant stimuli when the dorsal network is engaged in processing a task-relevant target (Corbetta et al., 2008; Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007; Todd et al., 2005; Shulman et al., 2003). The current findings show that the IPS is involved in T1 processing and that the IPL is related to successful T2 report. Thus, we assume that attentional processing of T1, as mediated by the IPS, induces a transient inhibition of IPL-related function. Because IPL activity is responsible for attentional disengagement and reorienting, this transient inhibition of IPL activity would have the effect of preventing disengagement and thereby increasing the AB effect. This assumption is consistent with recent models. Olivers and Meeter (2008) propose that blocking of T2 processing by the delay in T1 processing is not the direct cause of an AB deficit (Olivers, 2007; see also Duncan, Ward, & Shapiro, 1994). Instead, transient inhibition is triggered by a distractor following T1, and this results in a deficit in T2 processing. Additional evidence supporting this assumption may be obtained by clarifying the temporal relationship between the IPS and IPL activities using single-pulse TMS with high temporal resolution.

Note

1. No significant correlations were found between the luminance of the RSVP item and the magnitude of the AB in each of the conditions.

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