

Dissociable Neural Activations of Conscious Visibility and Attention

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Abstract

Recent neuroimaging evidence indicates that visual consciousness of objects is reflected by the activation in the lateral occipital cortex as well as in the frontal and parietal cortex. However, most previous studies used behavioral paradigms in which attention raised or enhanced visual consciousness (visibility or recognition performance). This co-occurrence made it difficult to reveal whether an observed cortical activation is related to visual consciousness or attention. The present fMRI study investigated the dissociability of neural activations underlying these two cognitive phenomena. Toward this aim, we used a visual backward masking paradigm in which directing attention could either enhance or reduce the object visibility. The participants' task was to report the level of subjective visibility for a briefly presented target object. The target was presented in the center with four flankers,

which was followed by the same number of masks. Behavioral results showed that attention to the flankers enhanced the target visibility, whereas attention to the masks attenuated it. The fMRI results showed that the occipito-temporal sulcus increased activation in the attend flankers condition compared with the attend masks condition, and occipito-temporal sulcus activation levels positively correlated with the target visibility in both attentional conditions. On the other hand, the inferior frontal gyrus and the intraparietal sulcus increased activation in both the attend flankers and attend masks compared with an attend neither condition, and these activation levels were independent of target visibility. Taken together, present results showed a clear dissociation in neural activities between conscious visibility and attention. ■

INTRODUCTION

Perceiving visual objects and raising their visual consciousness¹ is one of the main tasks of the visual system. People intuitively assume that it can be performed very efficiently, yet there are complicated mechanisms underlying it. Neuroimaging studies with PET, fMRI, and magnetoencephalography have reported that the lateral occipital complex (LOC) shows object-selective activation (Grill-Spector & Malach, 2004). For instance, the LOC responds more strongly when human participants view pictures of objects than when viewing textures, visual noise, scrambled objects, or scrambled Fourier phase information (Malach et al., 1995). Moreover, LOC activation does not reflect pre-conscious processes such as segmentation and grouping nor postconscious processes such as association of semantic knowledge and memory consolidation. LOC activation, rather, correlates with participants' visual consciousness in itself. For example, a target object can be rendered invisible

if it is immediately followed by a masking stimulus (visual backward masking; Breitmeyer, 1984). Interestingly, as visibility and object recognition performance is improved, the LOC shows increased activation (Noguchi & Kakigi, 2005; Avidan et al., 2002; Bar et al., 2001; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Vanni, Revonsou, Saarienen, & Hari, 1996).

Previous studies have found that, in addition to the LOC, activation in the fronto-parietal cortex is involved in conscious vision (Marois, Yi, & Chun, 2004; Rees, Kreiman, & Koch, 2002; Beck, Rees, Frith, & Lavie, 2001; Dehaene et al., 2001; Lumer & Rees, 1999; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998). However, other studies have also shown fronto-parietal involvement in attention (Pessoa, Kastner, & Ungerleider, 2003; Cabeza & Nyberg, 2000; Hopfinger, Buonocore, & Mangun, 2000; Wojciulik & Kanwisher, 1999; Corbetta et al., 1998; Corbetta, Miezin, Shulman, & Petersen, 1993). Other behavioral experiments have shown that even a salient object escapes from the observer's visual consciousness as long as their attention is directed away from the object (Simons & Chabris, 1999; Mack, Tang, Tuma, & Rock, 1992). This suggests that attention and visual consciousness are intricately related and difficult to distinguish in many cases. On the basis of these

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behavioral findings, previous neuroimaging studies used paradigms where directing attention enhanced conscious object recognition. However, this co-occurrence made it difficult to reveal whether an observed cortical activation is related to attention or consciousness.

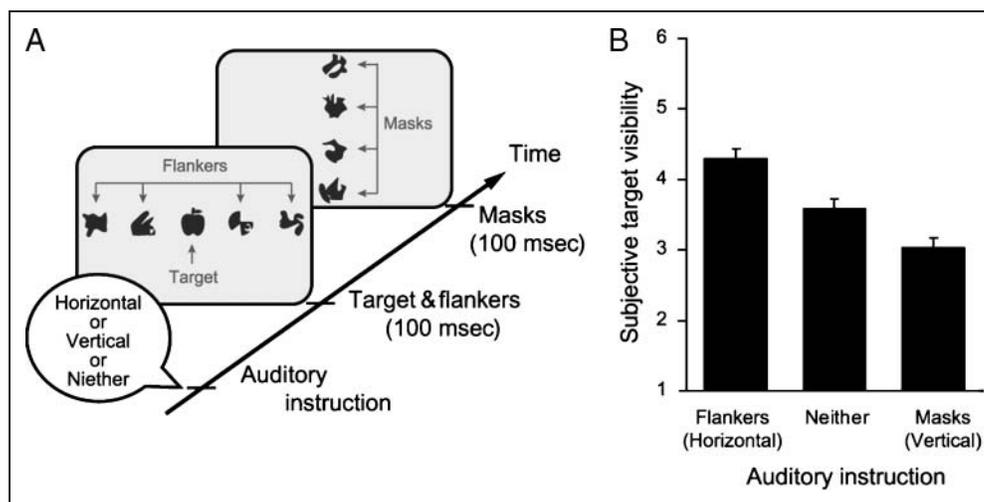
More recent behavioral studies have shown that attention and visual consciousness may be distinct processes (Koch & Tsuchiya, 2007; Lamme, 2003). For example, invisible objects sometimes can attract attention (Jiang, Costello, Fang, Huang, & He, 2006), and it is also possible to become conscious of an isolated object despite the near absence of top-down attention (Reddy, Wilken, & Koch, 2004; Li, VanRullen, Koch, & Perona, 2002). Furthermore, van Boxtel, Tsuchiya, and Koch (2010) reported direct evidence of the distinctiveness of attention from consciousness in visual afterimage experiments (a visual afterimage refers to an image staying in one's vision after exposure to the original image has ceased). Measuring the duration of the afterimage, they demonstrated that paying attention to the original image decreased the afterimage duration while consciously seeing the original image increased it. If attention and consciousness were identical, the same effect should have been observed between conditions. However, because attention and consciousness oppositely affected the same afterimage phenomenon, the researcher argued that they could be distinctive phenomena.

Although behavioral studies have begun to raise the dissociability of attention and visual consciousness, it remains unclear whether we can dissociate brain activations underlying these two cognitive phenomena. In the present fMRI study, we were especially interested in the neural dissociability of attention and visual consciousness in the occipital and fronto-parietal areas that have been reported to underlie both cognitive phenomena. Toward this aim, we used a

visual backward masking paradigm in which directing attention could either enhance or reduce the object visibility. The participants' basic task was to report the level of visibility for a target object (see Figure 1A) that was briefly presented in the center of the screen among four flankers in a horizontal row, two to the left of the target and two to the right, followed by the same number of masks in a vertical column. In addition to the basic task, the participants were further instructed to pay attention to the flankers, the masks, or neither before each trial. It has been shown that directing attention to the flankers reduces the masking effect (i.e., enhances target visibility) whereas directing attention to the masks increases the masking effect (i.e., attenuates target visibility; Boyer & Ro, 2007; Tata & Giaschi, 2004; Shelley-Tremblay & Mack, 1999; Ramachandran & Cobb, 1995). More precisely, in both the attend flankers and attend masks conditions, although participants are paying attention to an equal amount of visual objects (i.e., target + four flankers in attend flankers condition; target + four masks in attend masks condition), they experienced clearer visibility for the target object in the "attend flankers" condition but not in the "attend masks" condition. Therefore, by investigating the cortical region where the neural activity shows selective increases when participants attend flankers compared with when they attend masks, we can isolate the neural activity for conscious visibility independent of selective attention. Next, by observing the cortical region where the neural activity shows indiscriminate increases in both the attend flankers and attend masks conditions and comparing that to an "attend neither" condition, we can identify neural basis of selective attention. We used this experimental paradigm in which the stimulus presentation was the same across conditions to directly compare the neural activations for attention and conscious visibility from each other.

Figure 1. Stimuli, trial sequence, and behavioral results. (A) The participants' basic task was to report the level of subjective visibility for the target object presented in the center of the screen. Each trial began with an auditory instruction, asking participants to pay attention to the flankers (in horizontal row), masks (in vertical column), or neither. In the "neither" condition, participants were simply asked to do the task without explicitly attending to the flankers nor the masks. After 8 or 8.5 sec, the target was displayed in the center accompanying four flankers in a horizontal row

for 100 msec, which was followed by the same number of masks in a vertical column for 100 msec. The target-mask SOA was 100 msec. After observing the stimulus sequence, participants pressed a key to report the level of visibility of the target in a 6-point scale (1 = *invisible*, 6 = *clearly visible*). Note that in the experiment, the target was presented in gray on a black background. Here, colors are inverted for display purposes only. (B) Mean subjective target visibility ($\pm SE$) for each attentional condition. Large value indicates clear visibility.



METHODS

Participants

Ten² healthy right-handed adults (seven men, aged 22–27 years) with normal or corrected-to-normal vision participated. Participants gave written informed consent. The experiment was conducted in accordance with the ethical guidelines of the Declaration of Helsinki and approved by the Committee of Medical Ethics, Graduate School of Medicine, Kyoto University.

Stimuli and Procedure

The experiment was controlled by Presentation software (Neurobehavioral Systems, Inc., San Francisco, CA). Participants lay supine in the fMRI scanner with headphones and a button response device in their hands. They viewed stimuli through a mirror attached to the head coil. Figure 1A shows a schematic diagram of the experiment. Each stimulus subtended $1^\circ \times 1^\circ$ and was gray (0.54 cd/m^2) presented against a black background (0.10 cd/m^2). The target was displayed in the center of the screen accompanied by four flankers, two to the left and two to the right, in a horizontal row (separated by 2° and 4° from the target), followed by four masks in a vertical column (separated by 1° and 3° from the center). Targets were pictures of familiar animals, clothes, or vehicles, whereas flankers and masks were meaningless objects with a closed contour made by Endo, Saiki, Nakao, and Saito (2003).

The participants' basic task was to report their level of subjective visibility for the target. After 8 or 8.5 sec, the target was presented in the center of the screen with the four flankers in a horizontal row for 100 msec. It was followed by the same number of masks in a vertical column for 100 msec. The stimulus onset asynchrony (SOA) between the target + flankers display and the masks display was fixed at 100 msec. We chose the 100 msec SOA because we found the largest masking effect at this SOA in the pilot experiment. In addition to this basic task, three auditory instructions ("horizontal," "vertical," or "neither") further asked participants to pay attention to the flankers (in horizontal row), masks (in vertical column), or neither. In the neither condition, the participants were only required to do the basic task without attending to either the horizontal flankers or to the vertical masks. The auditory instructions were delivered through headphones 8 or 8.5 sec before target display (at the beginning of each trial). We used this extended event interval to isolate the BOLD signals related to visual target processes triggered by actual target presentation from the signals caused by the attentional preparation because of the auditory instructions. The former was the focus of the present study, whereas the latter was reported in Tsubomi et al. (2009). After the stimulus sequence, participants reported the level of target visibility in a 6-point scale (1 = *invisible*, 6 = *clearly visible*) by pressing a key. Response mapping of target visibility was counterbalanced across participants.

After 14 sec from the target display, the next auditory instruction was presented. The participants were instructed not to move their eyes from the center of the display until they rated the target visibility. The three different auditory instructions were presented in a pseudorandomized order (33 trials for each attentional condition). The participants completed three blocks of 33 trials each and rested for a few minutes between blocks.

fMRI Acquisition

The fMRI experiment was conducted in a 3-T MRI scanner with a head volume coil (Trio, Siemens, Erlangen, Germany). Functional images were acquired using a T2*-weighted, gradient-echo, EPI sequence with prospective motion correction capability (Thesen, Heid, Mueller, & Schad, 2000; repetition time = 3000 msec, echo time = 30 msec, field angle = 90° , field of view = $192 \times 192 \text{ mm}$, voxel size = $3.0 \times 3.0 \times 4.0 \text{ mm}$, slice number = 40 axial slices). Before the experimental session, high-resolution anatomical images were collected using a T1-weighted, magnetization-prepared, rapid gradient-echo sequence (repetition time = 2000 ms, echo time = 4.38 ms, field angle = 8° , field of view = $195 \times 240 \text{ mm}$, voxel size = $0.94 \times 0.94 \times 1$, slice number = 208 axial slices).

Image Processing and Analysis

Image processing and analysis were performed with SPM5 (Wellcome Department of Cognitive Neurology, London, U.K.) implemented in Matlab (MathWorks, Inc., Shervorn, MA). The functional images were corrected for differences in slice acquisition timing (Josephs & Henson, 1999) and were realigned to the first image for motion correction. These images were then anatomically normalized to the Montreal Neurological Institute (Quebec, Canada) template (Evans et al., 1993) and smoothed with an isotropic Gaussian kernel of 6-mm FWHM. Data from one participant was excluded from the analysis because of excessive head movement ($>1 \text{ mm}$). Individual analysis was performed with a fixed effect model, and group analysis was performed with a random effect model (Friston, Holmes, & Worsley, 1999). Statistical parametric maps of t statistics were calculated to identify voxels with event-related signal changes, using a general linear model (Friston et al., 1995). The model neural activity time course was convolved with a canonical hemodynamic response function.

We focused on the neural activity time-locked to the target presentation because our interest was the cortical region that takes the subjective visibility for the target object. To separately look at the neural basis of target visibility and attention, we made two contrasts. An "attend flankers–attend masks" contrast enabled us to isolate the cortical activation related to subjective target visibility independent of attention. This comparison was valid because participants paid attention to the same number of

visual objects in both attentional conditions (i.e., target + four flankers in the attend flankers condition; target + four masks in attend masks condition). The other contrast was the conjunction of “attend flankers–neither” and “attend masks–neither” (Friston, Holmes, Price, Büchel, & Worsley, 1999). This comparison was tested to investigate the neural basis of attention. Low-frequency noise was removed using a high-pass filter with cut offs ranging from 209 to 295 sec. The resulting t statistics were transformed to Z -score maps of normal unit distribution. The statistical threshold was set at $p < .001$ (without correction for multiple comparisons), corresponding to $Z > 3.20$. The Brodmann’s area was determined for each activation cluster by converting the Montreal Neurological Institute coordinates to Talairach coordinates (Talairach & Tournoux, 1988), using the Talairach Daemon software (Lancaster et al., 2000). To obtain a percent signal change in cortical activation, the BOLD signal intensity of a 3-mm sphere around a local maxima at event onset (target presentation) was subtracted 5–7.5 sec from that after event onset (peak intensity) in each trial for each participant. The local maxima was functionally defined as the voxel that demonstrated the highest Z values in each brain region. To correlate percent BOLD signal changes with conscious visibility, we first binned each individual’s BOLD amplitudes according to their subjective ratings for a given trial, and then, we averaged those amplitudes to produce the mean BOLD amplitude for each subjective rating. The resultant mean BOLD amplitudes for all participants were then regressed against participant’s subjective ratings.

RESULTS

Behavioral Data

We replicated the previous behavioral studies (Boyer & Ro, 2007; Shelley-Tremblay & Mack, 1999; Ramachandran & Cobb, 1995). Attention to the flankers (in horizontal row) enhanced the target visibility whereas attention to the masks (in vertical column) reduced it (Figure 1B). A one-factor ANOVA performed on the averaged target visibility demonstrated a significant effect of Auditory Instruction Type [$F(2, 18) = 18.28, p < .001, \eta^2 = .51$]. Paired-sample t tests demonstrated that the target visibility was higher in the attend flankers condition [$t(8) = 3.98, p < .01, r = .71$] and lower in the attend masks condition [$t(8) = 2.43, p < .01, r = .52$] when compared with the neither condition.

To further investigate the relationship between subjective rates of target visibility and target identification performance, we conducted a follow-up behavioral experiment outside the scanner. In that experiment, we asked new participants ($n = 10$) to verbally report the target identity and visibility. As a result, we found the attentional effect not only on the subjective visibility but also on task performance (target naming accuracy) [one-factor ANOVA, $F(2,$

$18) = 8.11, p < .001, \eta^2 = .37$]. The following paired-sample t tests demonstrated that the mean target accuracy was higher in the attend flankers condition [87%, $t(8) = 2.03, p < .05, r = .43$] and lower in the attend masks condition [76%, $t(8) = 2.03, p < .05, r = .43$] when each was compared with the neither condition (80%). We also found that all the participants rated “1” whenever they failed to report the correct target identity. This means that when the participants rated “2–6,” they could identify the target object. On the basis of this observation, we reanalyzed subjective ratings in the fMRI experiment, using only the trials rated “2–6.” The result showed that subjective rates of target visibility were still affected by the attentional conditions [one-factor ANOVA, $F(2, 18) = 30.92, p < .001, \eta^2 = .70$]. The mean subjective rating was higher in the attend flankers condition [mean = 3.64, $t(8) = 4.41, p < .01, r = .74$] and lower in the attend masks condition [mean = 2.25, $t(8) = 3.43, p < .05, r = .65$], when each was compared with the neither condition (mean = 2.86). This observation suggested that attention affected subjective rates of target visibility in trials rated “2–6,” leaving target identification performance intact.³

fMRI Data

First, we investigated the cortical activity time-locked to the target presentation in three conditions (Attend Flankers, Attend Masks, and Neither). As in Table 1, the frontal, parietal, and occipital cortex showed increased activity in all conditions.

We used a contrast of “attend flankers–attend masks” to identify the neural basis of target visibility. As seen in Figure 2, the occipito-temporal sulcus (OTS; BA 37; $x, y, z = 50, -62, -8; Z = 4.30$) showed increased activity in the attend flankers condition when compared with the attend masks condition. Figure 2 also shows the scatter plot of mean signal changes across trials in the OTS for each participant as a function of target visibility. In both attentional conditions, signal intensity increased as the subjective report of visibility increased (the regression slope in the “attend flankers” condition, $t(39) = 2.07, p < .05$; in the “attend vertical” condition, $t(39) = 2.09, p < .05$). Pearson’s correlation coefficient between subjective visibility and the BOLD signal changes was .32 in the attend flankers condition ($p < .05$) and .31 in the attend masks condition ($p < .05$).⁴

To identify the neural basis of selective attention, we performed a conjunction analysis to localize the commonly activated brain areas for both the attend flankers and attend masks conditions and compared them to the attend neither condition. As seen in Figure 3, five cortical regions in the fronto-parietal cortex showed the attention-related activation [right (R) and left (L) inferior frontal gyrus (IFG) and intraparietal sulcus (IPS); RIFG-1 (BA 47), $x, y, z = 34, 28, -8, Z = 4.19$; RIFG-2 (BA 45), $x, y, z = 50, 6, 20, Z = 4.13$; LIFG (BA 47), $x, y, z = -28, 26, -6; Z = 4.29$; RIPS (BA 7), $x, y, z = 40, -56, 46; Z = 4.37$; LIPS

Table 1. Brain Regions Exhibiting a Significant Increase in Activity Time-locked to the Target Presentation

Brain Region		BA	Flankers					Neither				Masks			
			x	y	z	Z Score	x	y	z	Z Score	x	y	z	Z Score	
Frontal lobe	IFG–inferior frontal sulcus	47	L	-32	24	-8	4.9	-38	16	-4	4.5	-28	24	-6	4.3
			R	52	20	-6	4.8	36	28	-6	3.7	44	24	0	4.7
	Precentral gyrus	44/6	L	-52	8	10	3.8					-48	2	26	3.7
			R	58	18	18	4.5								
	Superior frontal gyrus–cingulate gyrus	32/8	L	-8	10	48	4.6	-6	14	40	4.7	-16	10	42	3.2
			R	4	20	48	4.8	4	18	48	4.2				
	Middle frontal gyrus	46	R					50	36	18	3.8	54	30	28	3.7
10		R					38	38	16	3.9					
9		R					52	18	30	3.9	54	20	32	3.7	
	6	R	38	6	52	4.1					38	6	50	4.2	
Parietal lobe	Intraparietal sulcus	7	L	-28	-52	54	4.4	-40	-44	56	4.2	-38	-50	62	4.1
			R	42	-42	48	4.8	38	-48	50	4.3	42	-46	46	4.9
	Precuneus		L	-4	-80	40	4.5	-10	-72	40	3.9	-8	-76	50	4.2
			R					18	-66	26	4.3	14	-70	48	5.0
	Postcentral gyrus	2	L	-58	-22	30	4.6	-52	-24	42	5.0	-64	-20	32	4.5
		R									44	-24	40	4.1	
Temporal lobe	Fusiform gyrus	37	L								-46	-62	-14	3.7	
			R	48	-54	-10	4.9	46	-56	-16	4.3	48	-60	-12	4.6
	Middle temporal gyrus		R	46	-62	8	4.4								
	Parahippocampal gyrus	30	R								24	-38	4	4.6	
Occipital lobe	Fusiform gyrus–occipito–temporal sulcus	19	L					-30	-68	-12	5.1	-32	-74	-10	3.4
			R	24	-78	-12	4.6	22	-78	-12	4.0				
	Superior occipital gyrus	19	L	-32	-80	30	4.0								
			R	34	-70	30	3.6								
	Middle occipital gyrus	19	L					-32	-94	6	3.8	-26	-94	4	3.5
		R	52	-74	0	3.9	52	-78	-4	4.5	32	-82	-6	3.9	
Lingual gyrus–calcarine sulcus	17	L	-22	-88	0	4.7									
	18	R					26	-74	-6	4.3	23	-88	3	4.3	
Others	Thalamus		L	-16	-20	2	5.2	-12	-22	2	3.9	6	-28	-4	3.9
			R	10	-10	2	3.9	8	-14	-2	4.6	-6	-28	-4	4.3
	Corpus callosum		L					-4	-18	30	4.7	-8	-34	28	3.9
			R					6	-18	30	4.1				
Insula		L					-40	-8	12	5.1	-42	-8	14	4.0	

Coordinates (x, y, z) indicate the voxel of maximal significance in each brain region according to the stereotaxic coordinate system by Talairach and Tournoux (1988). BA = cytoarchitectonic fields designated Brodmann; L = left; R = right.

(BA 7), $x, y, z = -26, -52, 42, Z = 4.7$]. To validate that these areas were not related to subjective ratings of visibility, we calculated the mean signal changes of each participant in the five activated areas and plotted them as a function of target visibility (Figure 3). None of five regions showed significant signal changes depending on the level of

target visibility. Pearson's correlation coefficients between subjective visibility and the BOLD signal changes were as follows: .19 (RIFG-1), -.04 (RIFG-2), .03 (LIFG), .25 (RIPS), and .17 (LIPS) in attend flankers condition; -.17 (RIFG-1), .08 (RIFG-2), -.10 (LIFG), -.12 (RIPS), and -.18 (LIPS) in attend masks condition. All of these correlation coefficients

were nonsignificant ($p > .05$).⁵ To assure that these observations were related to the subjective visibility of target object, we reanalyzed the BOLD signal changes only with the trials rated “2–6,” in which the participants could identify the target object. We still found the same result as in the original analysis described above.⁶

In the fMRI experiment, we instructed participants not to move their eyes until they rated the target’s visibility. However, we did not measure participants’ eye movements during the experiment, and this left the possibility that differential eye movements may have contaminated the observed neural activation. To rule out this possibility, we conducted a follow-up experiment, measuring three participants’ eye movements while they perform the same task as in the main fMRI experiment. The results showed that participants were able to maintain their eye position at the center of the display (movements less than 1° away from the center) in 83% of trials. More importantly, the participants did not show any differences in eye movements between the three attentional conditions as well (see Supplementary Methods and Results). These findings rule out the oculomotor explanation of the observed differences in neural activation.

DISCUSSION

We obtained three main results in our study. First, behavioral results showed that attention could either enhance or reduce the target visibility. Directing attention to the flankers enhanced the target visibility (i.e., reduced the masking effect) whereas directing attention to the masks reduced the target visibility (i.e., enhanced the masking effect). In accordance with previous behavioral studies (Boyer & Ro, 2007; Tata & Giaschi, 2004; Shelley-Tremblay & Mack, 1999; Ramachandran & Cobb, 1995), we interpreted this result as follows; when the participants ad-

ditionally attended to flankers presented simultaneously with the target object, visual processing of the target object was saved from the backward masking. This resulted in the enhanced target visibility compared with the neutral (neither) situation. On the other hand, when the participants additionally attended to the masks presented after the target object, visual processing of mask objects in vertical column was promoted. This resulted in strengthening the backward masking effect and reducing the target visibility compared with the neutral (neither) situation. Second, fMRI analysis showed that the OTS (the putative LOC; Grill-Spector & Malach, 2004) represented the level of target visibility. The OTS showed increased activation in the attend flankers condition when compared with the attend masks condition. We conclude that difference in the contrast represents a difference in target visibility but not in selective attention because participants paid attention to the same number of visual objects in both attentional conditions (i.e., target + four flankers in attend flankers; target + four masks in attend masks). In fact, the OTS increased the signal intensity as participants reported clear target visibility in both attentional conditions. Third, fronto-parietal (IFG and IPS) areas showed the increased activation in both the attend flankers and attend masks conditions, when compared with the BOLD intensity in the attend neither condition. Importantly, it is unlikely that the signal intensity in these areas depended on the level of target visibility. Taken together, present results provide a clear dissociation of neural activations for the visibility of the task-related target stimulus and attention.

Occipital Activity and Conscious Object Recognition

The current study showed that the OTS activation positively correlated with the task-related target visibility

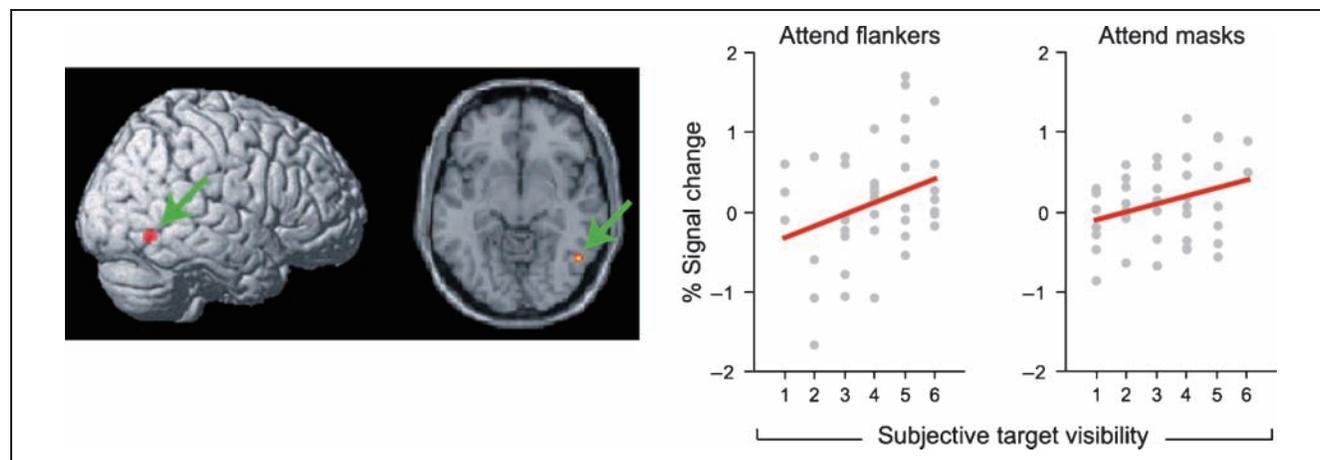


Figure 2. Cortical activation map and graphs associated with the level of target visibility: The contrast of “attend flankers–attend masks” time-locked to the target presentation is shown on the left. The right OTS showed the increased activity in the attend flankers condition. The statistical threshold was set to a p value of .001. The graphs show each participant’s mean percent fMRI signal change in the right OTS as a function of the level of target visibility in the attend flankers and attend masks conditions. The regression line is shown in red.

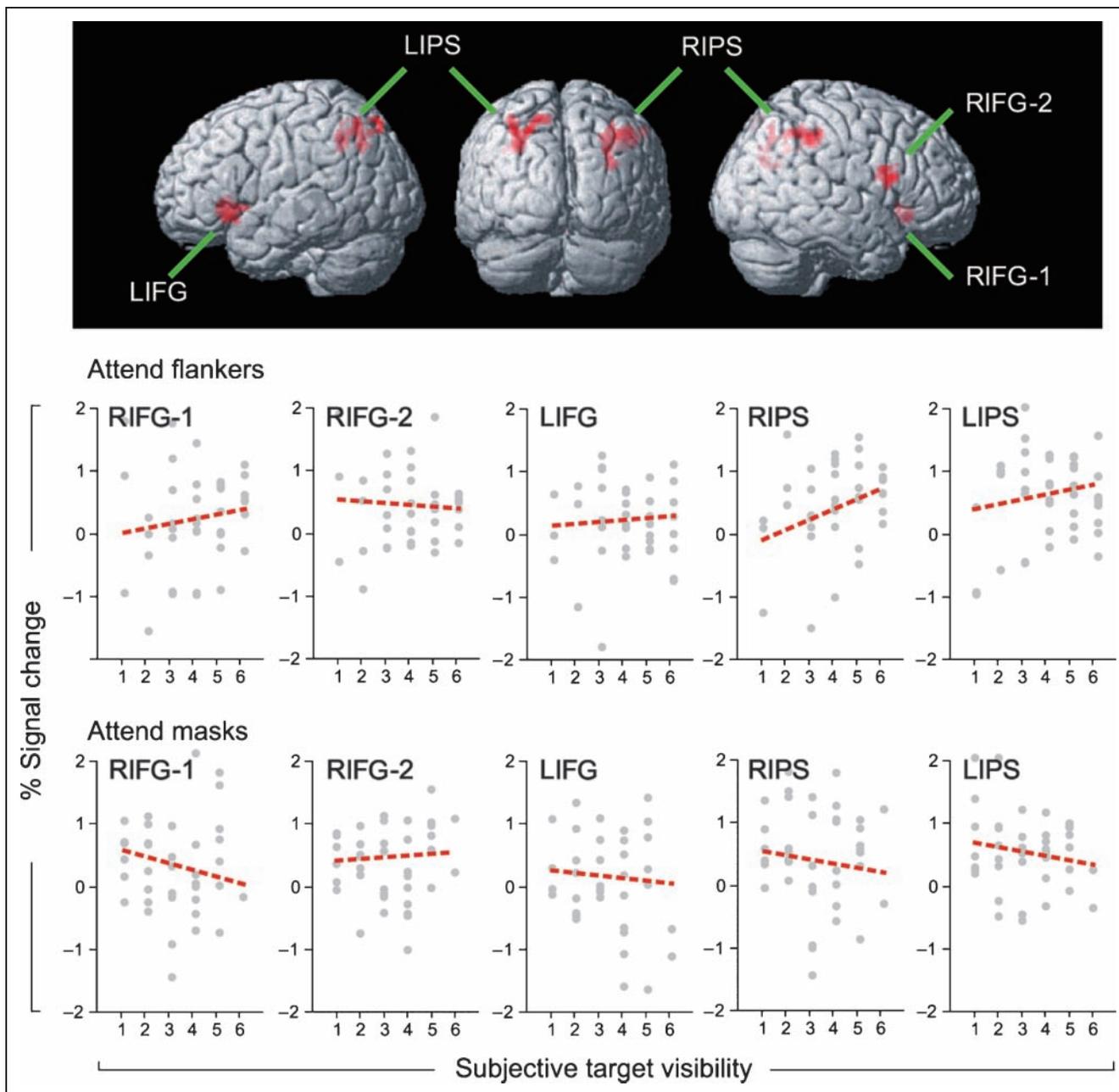


Figure 3. Cortical activation maps and graphs associated with top-down attention: The results of the conjunction analysis (“attend flankers–neither” and “attend masks–neither”) time-locked to the target presentation are shown above. Five cortical regions in the bilateral IFG and IPS showed increased activation in both the attend flankers and attend masks conditions when compared with the attend neither condition. The statistical threshold was set to a p value of .001. Graphs show each participant’s mean percent fMRI signal changes in the five regions as a function of the level of target visibility. None of five regions showed the signal changes depending on the level of target visibility (dashed regression lines indicate nonsignificant correlation, $p > .05$). L = left; R = right.

independent of attention. This result supports previous neuroimaging findings with the backward-masking paradigm. In previous studies, researchers found that activation in the occipital visual areas correlated with object recognition performance by varying the presentation duration of the target stimulus or extending the interval duration between the target and mask presentation (Noguchi & Kakigi, 2005; Avidan et al., 2002; Bar et al., 2001; Grill-Spector et al., 2000; Vanni et al., 1996). However, there has been

a possibility that occipital activation reflected postconscious processes such as association of long-term semantic knowledge and memory consolidation that contributed to successful recognition of the objects. Therefore, the true contribution of the OTS activation to subjective conscious visibility remained unclear. Thus, an important difference between these previous studies and the current study is that we successfully showed that attention affected the subjective target visibility, leaving the object identification

performance intact. These results strongly suggest that the activation in the OTS reflects the “subjective” assessment of visibility as well as the target identification performance in the previous studies. Another important point in the present study is that we used an identical stimulus presentation to compare different levels of subjective target visibility. Participants observed the same stimulus presentations in both the attend flankers and attend masks conditions. This ensures that the signal intensity in the OTS represents the subjective target visibility rather than the differences in physical stimulation. Although we observed the activation in the posterior occipital areas including the primary visual cortex in all three attentional conditions (see Table 1), these areas did not show any correlation with the target visibility. This result is also supported by the previous studies showing that the visibility of the task-related object is represented in the higher-visual areas like OTS but not in the lower visual areas (Avidan et al., 2002; Bar et al., 2001; Grill-Spector et al., 2000).

Present results are also in accordance with a study by Tse, Martinez-Conde, Schlegel, and Macknik (2005). They investigated the effect of attention to conscious perception while drawing attention away from the stimulus. The results showed that, in such a situation, the correlations of stimulus visibility were found solely in occipital areas, not in higher associative regions, and therefore, they argued that the mechanisms of conscious visual perception lie in the extrastriate cortex. The present study supports Tse et al.’s (2005) study because the occipital region of OTS was the only area that revealed a correlation with the level of target visibility.

The positive correlation between the OTS activation and target visibility showed right brain laterality in the present study. Although some neuroimaging studies reported the right occipital superiority in visual conscious perception (Lumer, Friston, & Rees, 1998; Vanni et al., 1996), other studies showed bilateral occipital correlation with visual recognition. We presented the target object in the center of the screen and participants performed the task with their eyes fixated on the center, suggesting that stimulus presentation condition cannot be attributed to the right lateralized effect. Clearly, further research is needed to reach any firm conclusions.

Fronto-parietal Activity and Attention

Previous neuroimaging studies reported fronto-parietal involvement in both attention (Pessoa et al., 2003; Cabeza & Nyberg, 2000; Hopfinger et al., 2000; Wojciulik & Kanwisher, 1999; Corbetta et al., 1993, 1998) and conscious vision (Marois et al., 2004; Rees et al., 2002; Beck et al., 2001; Dehaene et al., 2001; Lumer & Rees, 1999; Kleinschmidt et al., 1998). These studies used a behavioral paradigm in which directing attention enhanced object recognition performance. This made it difficult to reveal whether the observed cortical activation is related to attention or conscious object recognition. In the pre-

sent study, we could successfully dissociate attention and visual consciousness using the visual masking paradigm in which directing attention could either enhance or reduce target visibility. Simultaneously, we found attention-related activity in the fronto-parietal areas of IFG and IPS (in the conjunction analysis of “attend flankers–neither” and “attend masks–neither”). The level of activation in these areas did not show a dependency on subjective target visibility. These results strongly support the hypothesis that conscious perception is systematically associated with surges of parieto-frontal attentional activity causing top–down amplification (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2006; Dehaene, Sergent, & Changeux, 2003).

It is known that the increased IFG and IPS activation is involved in controlling distractor interferences (Caplan, McIntosh, & de Rosa, 2007; D’Esposito, Postle, Jonides, & Smith, 1999; Wojciulik & Kanwisher, 1999). In the present study, when participants attended to the flankers in a horizontal row, the masks in a vertical column were treated as distractors, and vice versa in the attend masks condition. Because conditions were randomized, participants were forced to switch their task set from trial to trial. This may indicate that IFG and IPS activities are involved in configuring attention to match with the concurrent task set.

Considering that many studies have reported occipital involvement in attention (Tsubomi et al., 2009; Hopfinger et al., 2000; Brefczynski & DeYoe, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Tootell et al., 1998), it may be odd that we found the attention-related activities only in the fronto-parietal areas. However, the present result does not exclude the occipital involvement in visual attention. In fact, when the threshold was reduced fivefold in the conjunction analysis (common to “attend flankers–neither” and “attend masks–neither”), we found significant occipital activity of bilateral lingual gyrus (RGL, $x, y, z = 28, -90, -4, Z = 2.62$; LGL, $x, y, z = -8, -78, -18; Z = 2.60$). An important observation to be noted here is that the BOLD signal change in the fronto-parietal areas was independent from the level of target visibility. Therefore, even if the OTS has some role in selective attention, our conclusion remains that the fronto-parietal areas function as selective attention and the level of visual consciousness is represented in the occipital area (OTS) but not in the IFG and IPS.

Dissociation of Visual Consciousness and Attention

Our fMRI results showed a clear dissociation between neural activations of attention and visual consciousness. The occipital area of OTS represented subjective target visibility and the fronto-parietal area of IFG and IPS represented selective attention. These results support the neuropsychological studies with brain-damaged patients. It is known that brain damage can induce two types of loss of visual consciousness. When the occipital cortex is damaged, the person feels a lack of visual consciousness

for sensory events located toward the contralesional side of space (Celesia, Bushnell, Cone-Toleikis, & Brigell, 1991; Horton & Hoyt, 1991). In contrast, when the fronto-parietal cortex is damaged, the person ignores sensory events located toward the contralesional side of space, which also results in a lack of visual consciousness (Mesulam, 1981; Heilman & Van Den Abell, 1980). One important difference between patients with occipital damage and those with fronto-parietal damage is that the former may consciously realize that their vision is restricted, but the latter hardly recognize their deficits. Even after they acknowledge that they miss things on the affected visual field, patients with fronto-parietal damage continue to neglect them (Driver & Vuilleumier, 2001). Interestingly, if their attention is attracted to an object they can be conscious of the ignored stimulus in the affected visual field. Smania et al. (1998) have reported interesting results of fronto-parietal damaged patients with the left visual field neglect. In visual tasks, the normal participants performed best at the center of the visual field, but the patients performed better within the right parafoveal field than in the center. On the basis of this finding they argued that the deficit might have originated from the patients' disability in controlling their attention, and thus their attention was biased toward the nonaffected visual field.

The present results support these studies by suggesting that the occipital and the fronto-parietal areas differently contribute to visual consciousness. We found that the occipital (OTS) activation positively correlates with the subjective visibility for the target object. On the other hand, the fronto-parietal areas (IFG and IPS) increased activation in relation to attention, and the activation levels in these areas are independent of the subjective visibility for the target. Taken together, we conclude that conscious visibility and attention are dissociable in human brain.

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Notes

1. Visual consciousness is referred to the content of consciousness (sometimes it is said as visual awareness), and not to states

of consciousness (e.g., wakefulness, dreamless sleep, or coma; van Boxtel et al., 2010).

2. The behavioral task and fMRI scan data in the present study were the same as those in our previous report (Tsubomi et al., 2009), but we time-locked to a different stimulus event for analysis. In our previous study, we analyzed the pretarget brain activity time-locked to the verbal instruction that was delivered long before the actual visual target presentation. The aim of that study was to relate the pretarget brain activity with the individual differences in the attentional effect on visual masking. On the other hand, the present study analyzed the fMRI data time-locked to the actual visual target presentation (a different event than what was reported in Tsubomi et al., 2009) to investigate the dissociability of neural activations underlying attention and conscious visibility.

3. We do not interpret these observations to suggest that subjective rates of target visibility are unrelated to target identification performance, rather, that attention affected subjective rates of target visibility, leaving target identification performance intact in the trials rated "2–6." We appreciate the reviewer's comment regarding this distinction.

4. 95% confidence interval of Pearson's correlation coefficient was $-.01$ to $.57$ in the attend flankers condition and $-.01$ to $.56$ in the attend masks condition.

5. 95% confidence interval of Pearson's correlation coefficient was as follows: in attend flankers condition, $-.12$ to $.47$ (RGFI-1), $-.27$ to $.34$ (RGFI-2), $-.28$ to $.33$ (LGFI), $-.07$ to $.51$ (RIPS), and $-.14$ to $.45$ (LIPS); in attend masks condition, $-.13$ to $.47$ (RGFI-1), $-.23$ to $.40$ (RGFI-2), $-.39$ to $.21$ (LGFI), $-.41$ to $.19$ (RIPS), and $-.46$ to $.13$ (LIPS).

6. The OTS activation levels positively correlated with the target visibility, whereas IFG and IPS activation levels were independent of the target visibility. Pearson's coefficient between the target visibility and activation levels in the OTS was $.41$ ($p < .05$) in the attend flanker condition and $.36$ ($p < .05$) in the attend masks condition. On the other hand, Pearson's correlation coefficients between the target visibility and activation levels were $-.08$ (RGFI-1), $.17$ (RGFI-2), $.00$ (LGFI), $.17$ (RIPS), and $.09$ (LIPS) in the attend masks condition and $-.06$ (RGFI-1), $.08$ (RGFI-2), $-.11$ (LGFI), $-.04$ (RIPS), and $-.23$ (LIPS) in the attend masks condition. All of these correlation coefficients in fronto-parietal areas were nonsignificant ($p > .05$).

REFERENCES

- Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., & Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *Journal of Neurophysiology*, *87*, 3102–3116.
- Bar, M., Tootell, R. B. H., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., et al. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron*, *29*, 529–535.
- Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience*, *4*, 645–650.
- Boyer, J., & Ro, T. (2007). Attention attenuates metacontrast masking. *Cognition*, *104*, 135–149.
- Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the "spotlight" of visual attention. *Nature Neuroscience*, *2*, 370–374.
- Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. Oxford, U.K.: Oxford University Press.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*, 1–47.

- Caplan, J. B., McIntosh, A. R., & de Rosa, E. (2007). Two distinct functional network for successful resolution of proactive interference. *Cerebral Cortex*, *17*, 1650–1663.
- Celesia, G. G., Bushnell, D., Cone-Toleikis, S., & Brigell, M. G. (1991). Cortical blindness and residual vision: Is the second visual system in humans capable of more than rudimentary visual perception? *Neurology*, *41*, 862–869.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*, 761–773.
- Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *The Journal of Neuroscience*, *13*, 1202–1226.
- Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, *10*, 204–211.
- Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J. F., & Poline, J. B. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*, 752–758.
- Dehaene, S., Sergent, C., & Changeux, J. P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proceedings of the National Academy of Sciences, U.S.A.*, *100*, 8520–8525.
- D'Esposito, M., Postle, B. R., Jonides, J., & Smith, E. E. (1999). The neural substrate and temporal dynamics of interference effects in working memory as revealed by event-related functional MRI. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 7514–7519.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.
- Endo, N., Saiki, J., Nakao, Y., & Saito, H. (2003). Perceptual judgments of novel contour shapes and hierarchical descriptions of geometrical properties. *Japanese Journal of Psychology*, *74*, 346–353.
- Evans, A. C., Collins, D. L., Mills, S. R., Brown, E. D., Kelly, R. L., & Peters, T. M. (1993). 3D statistical neuroanatomical models from 305 MRI volumes. In *Proceedings of the IEEE Nuclear Science Symposium on Medical Imaging* (pp. 1813–1817). Piscataway, NJ: IEEE, Inc.
- Friston, K. J., Holmes, A. P., Price, C. J., Büchel, C., & Worsley, K. J. (1999). Multisubject fMRI studies and conjunction analyses. *Neuroimage*, *10*, 385–396.
- Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). How many subjects constitute a study? *Neuroimage*, *10*, 1–5.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object selective activation is correlated to recognition in humans. *Nature Neuroscience*, *3*, 837–843.
- Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annual Reviews Neuroscience*, *27*, 649–677.
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, *30*, 327–330.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.
- Horton, J. C., & Hoyt, W. F. (1991). The representation of the visual field in human striate cortex. A revision of the classic Holmes map. *Archives of Ophthalmology*, *109*, 816–824.
- Jiang, Y., Costello, P., Fang, F., Huangd, M., & He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proceedings of the National Academy of Sciences, U.S.A.*, *103*, 17048–17052.
- Josephs, O., & Henson, R. N. (1999). Event-related functional magnetic resonance imaging: Modelling, inference and optimization. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *354*, 1215–1228.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*, 751–761.
- Kleinschmidt, A., Büchel, C., Zeki, S., & Frackowiak, R. S. J. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London, Series B*, *265*, 2427–2433.
- Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, *11*, 16–22.
- Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, *7*, 12–18.
- Lamme, V. A. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*, 494–501.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, *10*, 120–131.
- Li, F. F., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 9596–9601.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, *280*, 1930–1934.
- Lumer, E. D., & Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 1669–1673.
- Mack, A., Tang, B., Tuma, R., & Rock, I. (1992). Perceptual organization and attention. *Cognitive Psychology*, *24*, 475–501.
- Malach, J. B., Reppas, R. R., Benson, K. K., Kwong, H., Jlang, W. A., Kennedy, P. J., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 8135–8139.
- Marois, R., Yi, D. J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron*, *41*, 465–472.
- Mesulam, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, *10*, 309–325.
- Noguchi, Y., & Kakigi, R. (2005). Neural mechanisms of visual backward masking revealed by high-temporal resolution imaging of human brain. *Neuroimage*, *27*, 178–187.
- Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: From modulation of sensory processing to top-down control. *The Journal of Neuroscience*, *23*, 3990–3998.
- Ramachandran, V. S., & Cobb, S. (1995). Visual attention modulates metacontrast masking. *Nature*, *373*, 66–68.
- Reddy, L., Wilken, P., & Koch, C. (2004). Face-gender discrimination is possible in the near-absence of attention. *Journal of Vision*, *4*, 106–117.
- Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, *3*, 261–270.

- Shelley-Tremblay, J. F., & Mack, A. (1999). Attention modulates metacontrast masking. *Psychological Science, 10*, 508–515.
- Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattention blindness for dynamic events. *Perception, 28*, 1059–1074.
- Smania, N., Martini, M., Gambina, G., Tomelleri, G., Palamara, A., Natale, E., et al. (1998). The spatial distribution of visual attention in hemineglect and extinction patients. *Brain, 121*, 1759–1770.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-Dimensional proportional system: An approach to cerebral imaging*. New York: Thieme.
- Tata, M., & Giaschi, D. (2004). Warning: Attending to a mask may be hazardous to your perception. *Psychonomic Bulletin & Review, 11*, 262–268.
- Thesen, S., Heid, O., Mueller, E., & Schad, L. R. (2000). Prospective acquisition correction for head motion with image-based tracking for real-time fMRI. *Magnetic Resonance in Medicine, 44*, 457–465.
- Tootell, R. B., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., et al. (1998). The retinotopy of visual spatial attention. *Neuron, 21*, 1409–1422.
- Tse, P. U., Martinez-Conde, S., Schlegel, A. A., & Macknik, S. L. (2005). Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2. *Proceedings of the National Academy of Sciences, U.S.A., 102*, 17178–17183.
- Tsubomi, H., Ikeda, T., Hanakawa, T., Hirose, N., Fukuyama, H., & Osaka, N. (2009). Connectivity and signal intensity in the parieto-occipital cortex predicts top-down attentional effect in visual masking: An fMRI study based on individual differences. *Neuroimage, 45*, 586–596.
- van Boxtel, J. J. A., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences, U.S.A., 107*, 8883–8888.
- Vanni, S., Revonsou, A., Saarienen, J., & Hari, R. (1996). Visual awareness of objects correlates with the activity of right occipital cortex. *NeuroReport, 6*, 183–186.
- Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron, 23*, 747–764.