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Attentional Set for External Information Activates the Right Intraparietal Area

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Abstract

Visual attention can be allocated to a location or an object by using two different types of information: internal information and external information. The results of recent psychological studies [e.g., Bacon and Egeth, *Percept. Psychophys.*, 55 (1994) 485] suggest that an observer's attentional set determines how these two kinds of information are used in visual tasks. In this study, we measured brain activities during two modes of visual search; one is the feature search mode, in which an attentional set for knowledge of a target item (internal information) is used, and the other is the singleton detection mode, in which an attentional set for oddness in the visual scene (external information) is used. We found extended activation in the frontal and parietal areas for both search modes. In addition, a direct comparison of brain activity during the singleton detection mode and the feature search mode revealed that the areas around the right intraparietal sulcus were more involved in the attentional set for oddness. These results suggest that the human right intraparietal cortex is related to the attentional set for external information.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Attentional set; functional MRI; attentional capture; visual search

1. Introduction

Humans can usually see what they want to see. Such an ability to select an object, as one of the main functions of visual attention, enables humans to process visual information efficiently. In contrast, visual saliency, such as a feature singleton, a novelty, visual conspicuity, and the discontinuity of a visual scene, can automatically attract visual attention irrespective of our intention. That is, two different kinds of information affect our visual attention: internal information and external information.

Several psychological studies have reported on the interaction between the two kinds of information processing. Theeuwes [35] suggested that the most salient item in the visual display always captures attention in a stimulus-driven way [see also 21, 34, 36, 38, 39]. In the shape condition of his experiment, a color singleton (which is differentiated from other items in color dimension) always captures attention although the search target was a circle among squares. Conversely, in the color condition, in which the search target was a red item among green items, a shape singleton (a circle among squares) did not capture attention. Theeuwes ascribed this asymmetry in attentional capture to the difference in the extent of saliency between a color singleton and a shape singleton and concluded that the most salient item in the visual display always captures attention irrespective of the current search target.

However, the results of other recent studies suggested that involuntary attentional capture by a salient item occurs only when the

salient item is consistent with the task demand or an observer's attentional set [1, 11, 12, 18, 41]. For instance, Bacon and Egeth [1] showed that an observer's attentional set determines whether the salient item captures visual attention or not. In their third experiment, the salient distractor, which did not match the attentional set, did not capture attention even when the stimulus configuration was exactly the same as that of their first experiment in which they replicated the result of Theeuwes [35]. They discussed the discrepancy between Theeuwes's and their own results as follows. Observers might use the two different visual search modes according to the task demand. One is the feature search mode in which an observer's attentional set is toward a specific feature and visual search depends on observer's knowledge or expectation about the target (e.g., a representation of a circle held in the working memory). The other is the singleton detection mode in which an observer's attentional set is toward the oddness in the visual scene and visual search depends on the sensory input. The singleton detection mode is more susceptible to interference from singletons on irrelevant dimensions because not only the target item but also the singletons in the irrelevant dimensions are consistent with the attentional set for oddness. In the experiment of Theeuwes, although the search target was defined as a specific shape (a circle), the target was also a shape singleton. Therefore, observers might use the singleton detection mode rather than the feature search mode.

In short, the difference in the attentional set between the two visual search modes greatly affects control of spatial attention during visual search

tasks. Thus, identifying the brain areas related to the two visual search modes will clarify the neural basis of the attentional set that controls the interaction between internal and external information in visual processing. In the present study, we used functional MRI to measure brain activity during the feature search and singleton detection modes of visual search.

2. Experiment 1

In the first psychological experiment, we measured behavioral indices to determine the following: (a) whether the task difficulty and search efficiency in the feature search task (FS) and in the singleton search task (SS) are the same; and (b) whether these tasks induce the feature search mode and the singleton detection mode, respectively. In Exp. 1a, we varied the display set size to determine the search efficiency. We then added a salient distractor to directly assess which search mode was used in each task, in Exp. 1b.

2. 1. Method

2. 1. 1. Subject

Twelve volunteers participated in both Exp. 1 and Exp. 2. All had normal or corrected normal vision. Informed consent was obtained from all the subjects following procedures of the Declaration of Helsinki and approved by the Ethical Committee of the Communications Research Laboratory. All were right-handed as determined by the Edinburgh

Handedness Inventory [27].

Seven subjects participated in Exp. 2 after Exp. 1; the remaining subjects performed Exp. 2 first. Because the latter five subjects participated in the pilot experiment of Exp. 1 prior to Exp. 2, all 12 subjects had sufficient practice in the search tasks before participating in Exp. 2.

2. 1. 2. Stimulus

The stimulus was generated and controlled using a personal computer (PC9821, NEC, Japan). The stimulus displays consisted of several objects (6, 8, and 10 objects in Exp. 1a; eight objects in Exp. 1b.) located at equal intervals along an imaginary circle (8° radius in visual angle) on a black background. We used a square with 1.5° sides, a diamond (a square rotated 45°), and a triangle with 2° sides as objects. There were horizontal or vertical gray (approximately 2 cd/m^2) line segments (0.8°) inside each object. The objects were shown in red (approximately 4 cd/m^2) or in green (approximately 5 cd/m^2). Additionally, a gray fixation cross (1°) was always presented in the center of the imaginary circle.

2. 1. 3. Task design

Experiment 1 was comprised of two parts (1a and 1b), each of which had two experiment factors. Both Exps. 1a and 1b had a search-type factor [a feature search task (FS) and a singleton search task (SS)]. Additionally, Exp. 1a had a set-size factor (6, 8, and 10) and Exp. 1b had a salient distractor factor (a salient distractor was either presented or not).

The target-defining attribute was a shape singleton in the SS, and a

specific shape in the FS. Therefore, during the SS, we changed the target shape and the background shape pseudo-randomly in the trials; the subjects searched for a diamond among several squares in half of the SS trials and for a square among several diamonds in the other half of the SS trials. In contrast, in the FS, the subjects always searched for a diamond among the objects, including several squares as background objects and one triangle as a shape distractor. This shape distractor ensured that the target was not a shape singleton in the FS.

In Exp. 1a, the stimulus display contained 6, 8, and 10 green objects. In Exp. 1b, the set size was always eight, and one of the background objects was shown in red as a task-irrelevant but salient distractor in half of the trials. The stimulus configuration used in Exp. 1 is depicted in Figures 1a-1d.

2. 1. 4. Procedure

The subjects sat in front of the computer display in a dim room wearing an eye-mark recorder (SR Research, Ltd., Eye Link) to record their eye movements during the experiments. Experiment 1 was divided into two experimental sessions. One was for the SS and the other was for the FS. The order of the search tasks was counterbalanced among the subjects.

Each session consisted of four separate blocks. We assigned the first three blocks to Exp. 1a, in which the display set size was varied, and the last block to Exp. 1b. The order of the set size was counterbalanced across the sessions and among the subjects.

Prior to each session, the subjects were given a practice session of 100 trials. In this session, the subjects received feedback about the trajectory of their eye movements after their manual response in each trial to minimize the eye movement. At the end of the practice session, all of the subjects were able to fixate their eyes on the fixation cross throughout the visual search.

At the beginning of each trial, a fixation cross was presented in the center of the screen. After a subjects' fixation lasting 100 ms, a stimulus set was presented and it remained on the screen until the manual response was recorded. After a 500-ms inter-trial interval, a fixation cross for the next trial was presented.

2. 2. Results and Discussion

2. 2. 1. Experiment 1a

The reaction time, the error rates, and the saccade rates in Exp. 1 are shown in Table 1. Three separate two-way analyses of variance (ANOVAs) on the correct mean RTs, error rates, and saccade rates revealed neither a significant main effect [RT: $F(1, 11) = 0.69$, $F(2, 22) = 1.07$; error rate: $F(1, 11) = 2.19$, $F(2, 22) = 1.88$; saccade rate: $F(1, 11) = 0.74$, $F(2, 22) = 1.26$; for the search type and the set size, respectively] nor interaction between the two factors [RT: $F(2, 22) = 0.35$, error rate: $F(2, 22) = 2.27$, saccade rate: $F(2, 22) = 1.54$].

The result for the set size clearly suggests that the subjects could search for the target efficiently in both tasks. Thus, we concluded that the search efficiency in the FS and SS tasks was the same. Furthermore, the

result for the search type (FS vs. SS) showed that the task difficulty in the FS and SS tasks was also the same.

2. 2. 2. Experiment 1b

An ANOVA for the correct mean RTs showed a significant main effect of the salient distractor [$F (1, 11) = 44.19, p < .00004$] and significant interaction between the search type and the salient distractor [$F (1, 11) = 6.23, p < .05$]. A simple effect analysis of the interaction showed significant effects of the salient distractor on both the SS ($p < .01$) and the FS ($p < .05$) and a significant difference between the SS and FS when the salient distractor was presented ($p < .01$). These results show that the task-irrelevant salient object distracted the visual search in both search tasks and the distraction effect was greater in the SS than in the FS.

In the FS, the feature search strategy could not perfectly suppress the attentional capture by the color singleton distractor. However, the distraction caused by the salient distractor was significantly greater in the SS than in the FS. This result suggests that, in the FS, the subjects used the feature search mode that attenuated the disruption by the task-irrelevant saliency. Thus, we concluded that the singleton detection mode was dominant in the SS, and the feature search mode was dominant in the FS.

In Exp. 1b, the subjects made more errors in the SS than in the FS [$F (1, 11) = 16.99, p < .02$]. However, neither the main effect of the salient distractor nor the interaction between the search type and the salient distractor was significant [$F (1, 11) = 4.10$ for the distractor factor, $F (1, 11)$

= .26 for the interaction between the two]. The saccade rates did not show any significant result [$F(1, 11) = .05$, $F(1, 11) = 3.06$ and $F(1, 11) = .40$, for the search type, salient distractor, and the interaction between the two].

3. Experiment 2

In Exp 1, we found that both the task difficulty and search efficiency in the FS and SS were the same and our procedure could make the subjects use different visual search modes in the FS and SS. In Exp. 2, we measured the brain activity during those two search tasks by using fMRI.

3. 1. Method

3. 1. 1. Stimulus

The stimulus in Exp. 2 was identical to that in Exp. 1a, except for the following. First, the display set-size was fixed to eight. Second, the control condition, in which only line segments were presented, was added (see the following “Task design” section for details).

3. 1. 2. Task design

In addition to the FS and SS, control tasks in which only line segments were presented in the constant orientation (vertical or horizontal, see Fig. 1e) were conducted. Subjects were asked to answer the line orientation as in the FS and SS. However, in the control tasks, they did not need to allocate their attention to the specific location, because eight line segments in the control tasks always oriented in one direction. Therefore, the

control tasks were expected to distinguish brain activity related to undesirable cognitive activity (e.g., discrimination of line orientation, button pressing, and eye fixation) from brain activity related to the control of the spatial attention.

All the subjects had two sessions each of which contained three repetitions of experimental blocks. In each experimental block, they first performed the control tasks (C) in 36 trials. Subsequently, they performed two test search tasks (FS and SS) in 36 trials. Thus, they performed 216 trials for each task. Each experimental block was preceded by a 12-sec cue stimulation period in which cue symbols were presented at the center of the display to inform the subjects of the type of task that would be executed in the subsequent block (a fixation cross for the control condition; a triangle for the FS; the combination of a square and a diamond for the SS, see Fig. 1f). The order of the two test search tasks was counterbalanced among the blocks and across the sessions.

Differently from Exp. 1, the duration of the trial was fixed to 2 sec in Exp. 2 to equate the number of trials across conditions and subjects. Thus, each experimental block lasted for 72 sec. At the beginning of the trial, a fixation cross was presented for 200 ms. Subsequently, the stimulus set was given and lasted for 1800 ms irrespective of the subject's response to equate the amount of visual stimulation in the search tasks. Immediately after the stimulus set disappeared, a fixation cross for the next trial was presented.

We measured the RTs and error rates to verify that the search difficulty in each search task was the same.

3. 1. 3. Functional MRI Procedure

The subjects lay in a 1.5 Tesla MAGNETOM Vision scanner (Siemens Medical Systems, Erlangen, Germany) holding a response key in each hand with their eyes fixated on the screen at a distance of 27 cm via a tilted mirror. Both the mirror and the screen were mounted on the head coil of the MRI scanner. A stimulus was projected onto the screen by using an LCD projector (DLA-G10, Victor, Japan). The subjects' head movements were minimized by using a bite bar made with each subject's dental impression.

Thirty-two T2* weighted [repetition time (TR) 4000 ms, echo time (TE) 55.24 ms, flip angle (FA) 90°] axial images were acquired to cover almost the whole brain. The pixels were 4 x 4 mm, and the slices were 4-mm thick with no slice gap.

To accurately determine the location of activated areas, T1 weighted high-resolution structural images were acquired at the same position as the functional images (TR 480 msec, TE 6 msec, FA 90°, pixel size 1 mm, slice thickness 4 mm, no gap).

3. 1. 4. Functional MRI analysis

We used SPM99 software (Wellcome Department of Cognitive Neurology, London, UK) for the preprocessing and statistical analysis of the functional images. All functional images for each subject were realigned to the first image in the session to correct for the head movement in the scans. Then, the structural images were coregistered to the functional images to

put both types of images into the same space. All the images were spatially normalized to the MNI template (Montreal Neurological Institute, Quebec, Canada). In the final step of preprocessing, the functional images were spatially smoothed with an 8-mm Gaussian kernel.

In the first level of the statistical analysis, we analyzed the functional images individually by using a general liner model. Three task blocks were modeled by using the boxcar function convolved with the heamodynamic response function in SPM99. We added a temporal high-pass filter having a 512-sec cut-off period and a low-pass filter by using the heamodynamic response function to exclude low-frequency noise and temporal autocorrelation, respectively. Then, we performed three planned subtractions. The first two subtractions were direct comparisons between the two search conditions, that is, FS – SS, SS – FS. The third subtraction was the (FS +SS) – C subtraction to reveal the mean activation of the FS – C and the SS – C subtractions.

In the second level, we performed group analyses with the random effect model by using contrast images obtained from the individual analyses. The statistical significance of the activated regions in the paired t tests was assessed by using both a height threshold ($T > 3.11$ corresponding to $p < .005$, uncorrected for multiple comparisons) and a spatial extent threshold ($p < .05$, corrected for multiple comparisons).

3. 2. Results and Discussion

3. 2. 1. Behavioral Data

Table 2 shows the mean correct RTs and error rates for ten subjects

(we could not obtain the behavioral results for two subjects because of the failure to record their responses). Repeated measures ANOVA showed a significant main effect of the condition [RT: $F(9) = 66.39$, $p < .10^{-6}$; error rate: $F = 9.83$, $p < .002$]. Post hoc analysis showed that both the RT and the error rate for the control condition were smaller than those for the other two conditions [RT: $p < .0002$ for FS vs. C, $p < .0002$ for SS vs. C; error rate: $p < .005$ for FS vs. C, $p < .002$ for SS vs. C]. However, no significant difference was found between the FS and SS [RT: $p = .79$; error rate: $p = .38$].

3. 2. 2. Functional Data

Figure 2 shows the activated regions obtained from the results of a group analyses. Activation maps from three planned comparisons were overlapped to a normalized structure image of a given subject in different color maps. Table 3 shows the corresponding coordinates of the significant activated areas.

3. 2. 2. 1. Singleton Search vs. Feature search

In group analysis, one area of significance appeared in the SS – FS subtraction. The right intraparietal area was significantly more active during the SS than during the FS (Fig. 2). This activation extended from the post central gyrus (56, -22, 20) to the transverse occipital sulcus (32, -86, 26) through the anterior (38, -34, 38) and posterior (32, -64, 46) parts of the IPS (see Table 3). Figure 3a shows the result obtained from a representative single subject (Sub. 11), revealing activations in the bilateral FEF and the

bilateral intraparietal areas, both of which are well known as the attention-related brain region. All the regions were highly active both in the FS and in the SS. Furthermore, the right intraparietal area was more active in the SS than in the FS. This difference in activation maps between the right intraparietal area and the other three regions is also discernible in the raw data. Figure 3b shows the percent change for the MR signal for this subject in the bilateral FEFs and the bilateral intraparietal areas. MR signals increased equally during the FS and the SS in the bilateral FEFs and the left intraparietal area (upper six figures). In contrast, in the right intraparietal area, the MR signal increments during SS were larger than those during the FS (lowest two figures). Similar intraparietal activation patterns are also visible in other individual analyses. Figure 4 shows the intraparietal activations for the SS – FS subtractions in the seven individual analyses [$p < .001$ uncorrected for multiple comparisons, inclusively masked by the $(FS + SS) - C$ subtractions ($p < .05$ uncorrected for multiple comparisons); the other five subjects did not show significant intraparietal activation in this comparison]. The intraparietal activation clearly lateralized to the right hemisphere in Sub. 1, Sub. 8, Sub. 9, and Sub. 11.

Although the precise homology between the human and monkey parietal areas is still unclear, the extended cluster revealed here possibly includes homologies of monkey AIP, VIP, LIP, and V3A [9, 16, 24, 30]. These results suggest that the parietal activation by singleton search has strong laterality in the right hemisphere.

In contrast to the SS – FS subtractions, the FS – SS subtractions did

not show any significant activation.

3. 2. 2. Brain Activity during Visual Search Tasks

The (SS + FS) – C subtractions showed several areas of extended cortical activation (Fig. 2): the bilateral frontal eye field (FEF: the junction between the superior frontal sulcus and the precentral sulcus), the bilateral ventral premotor area (precentral gyrus), the anterior cingulate cortex (ACC), the bilateral intraparietal area, and the bilateral visual cortices. Additionally, this subtraction revealed subcortical activation around the bilateral pulvinar (Table 3). The overall activation pattern revealed in this subtractions, except for the bilateral visual cortices, was consistent with the attention- and saliency-related brain activity reported in a number of recent imaging [7, 10, 13, 23, 25, 26, 28, 29, 32] and electrophysiological [2-4, 14, 15, 22, 31, 37] studies. The bilateral activations in the visual cortices would reflect the difference in the visual stimulation between the control condition and the two test conditions.

4. General Discussion

We measured the brain activity involved in the control of visual attention during two different visual search tasks. In these tasks, the task difficulty and search efficiency were the same although the search strategies were different. We focused on comparing the brain activities during the two search tasks.

Although there was no difference between behavioral indices in the FS

and SS in Exp. 1 and Exp. 2, the right intraparietal activation was significantly stronger in the SS than in the FS. No other significant difference between the FS and SS was observed. These results clearly show that the right intraparietal area is closely related to the singleton detection mode of visual search, which depends on sensory input rather than an observer's knowledge about the target item.

Our task required observers to use several cognitive stages to produce a correct response. That is, to set an attentional set that corresponds to the task demands; to search and detect the target item by depending more on either internal information (the feature search mode) or sensory input (the singleton detection mode); to direct spatial attention to the target item; to identify line orientation, and finally to press the button using the correct hand. The first two stages of the task, which were closely related to the attentional set, could affect the difference in the right intraparietal activation, i.e., the attentional set for a specific shape (in the FS) or oddness in the visual scene (in the SS), search and detection of the target by using internal (in the FS) or external information (in the SS). However, not only the difference in the attentional set but also a subtle difference in sensory input could cause the different activation, because the target item in the SS, which might be more salient than that in the FS, could activate saliency-processing brain areas (e.g., saliency map) more strongly than that the FS did.

It is difficult to separate brain activities caused by the attentional set from those caused by sensory input because we used a block-design

procedure for our fMRI experiment. However, several previous studies would be helpful for further discussion of the present results. Corbetta and Shulman [8] reviewed recent event-related fMRI studies addressing visual attention and suggested that two distinct brain networks control visual attention differently. One network, which includes parts of the intraparietal area and the superior frontal cortex, is related to intentional selection for stimuli and response (they termed it the *dorsal frontoparietal network*). The other network, which includes the temporoparietal cortex and the inferior frontal cortex, is largely lateralized to the right hemisphere and detects behaviorally relevant, salient stimuli (the ventral right frontoparietal network). According to their review, most of the brain activities obtained in the present study were involved in the dorsal frontoparietal network: the bilateral FEF activation and the bilateral intraparietal activation in both the FS – C and the SS – C subtractions, the right intraparietal activation in the SS – FS subtractions [see 5, 17, 20, 33]. Conversely, no activation was obtained in the ventral right frontoparietal network even in the FS – C and SS – C subtractions. Therefore, intentional control of attention (i.e., attentional set), rather than sensory input, would be feasible as the source of the right intraparietal stronger activation during the SS even though the activation was strongly lateralized to the right hemisphere.

Then, why was the intraparietal activation obtained in the SS – FS subtraction lateralized to the right hemisphere? Similar lateralization in the intraparietal area was reported by Kim et al. [19] for the two kinds of spatial attention tasks; the intraparietal activation was strongly lateralized to the

right hemisphere in the exogenous cueing task, but not lateralized in the endogenous cueing task. Although the authors did not point it out explicitly in their procedure, the subjects might change their attentional set depending on the task. In the exogenous cueing task, subjects probably made an attentional set for the target position (fully external information) because the peripheral cue did not indicate the correct target position. On the other hand, in the endogenous cueing task, subjects might make an attentional set for interpreting the central arrow cue (internal information) because the cue informed them of the correct target position in 80% of the trials. Therefore, their results could involve brain activities reflecting not only the difference in shift of spatial attention but also the difference in the attentional set. Combining the result of Kim et al. [19] and our present study, we can suggest one possible account for the right hemisphere dominance in the intraparietal area. That is, the intraparietal activation involved in an attentional set, which is considered to be distributed to the bilateral hemisphere equally [8], could be stronger in the right hemisphere when the attentional set is directed to the external information (e.g., the SS in the present study; the exogenous cueing task in Kim et al.'s study).

In conclusion, we investigated the brain regions related to two modes of visual search: the feature search mode and the singleton detection mode. A direct comparison between brain activities during the singleton detection mode and the feature search mode revealed that the area around the right intraparietal sulcus was more active during a search with an attentional set for external information. However, because we focused only on the shape

dimension in the present study, it is difficult to say whether the intraparietal activity revealed in the present study reflects the attentional set for oddness in the shape dimension or for more general external information. Further study using other visual attributes such as motion and color are needed [6].

- [1] W.F. Bacon and H.E. Egeth, Overriding stimulus-driven attentional capture. *Percept. Psychophys.* 55 (1994) 485–496.
- [2] N.P. Bichot and J.D. Schall, Effects of similarity and history on neural mechanisms of visual selection. *Nat. Neurosci.* 2 (1999) 549–554.
- [3] N.P. Bichot, J.D. Schall, and K.G. Thompson, Visual feature selectivity in frontal eye fields induced by experience in mature macaques. *Nature* 381 (1996) 697–699.
- [4] C. Constantinidis and A. Steinmetz, Neuronal responses in area 7a to multiple-stimulus displays: I. Neurons encode the location of the salient stimulus. *Cereb. Cortex* 11 (2001) 581–591.
- [5] M. Corbetta, J.M. Kincade, J.M. Ollinger, M.P. McAvoy, and G.L. Shulman, Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3 (2000) 292–297.
- [6] M. Corbetta, F.M. Miezin, S. Dobmeyer, G.L. Shulman, and S.E. Petersen, Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* 248 (1990) 1556–1559.
- [7] M. Corbetta, G.L. Shulman, F.M. Miezin, and S.E. Petersen, Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* 270 (1995) 802–805.
- [8] M. Corbetta and G.L. Shulman, Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3 (2002) 201–215.
- [9] J.C. Culham and N.G. Kanwisher, Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.* 11 (2001) 157–163.
- [10] T. Donner, A. Kettermann, E. Diesch, F. Ostendorf, A. Villringer, and S.A. Brandt, Involvement of the human frontal eye field and multiple parietal areas in covert visual selection during conjunction search. *Eur. J. Neurosci.* 12 (2000) 3407–3414.
- [11] C.L. Folk and R. Remington, Can new objects override attentional control settings? *Percept. Psychophys.* 61 (1999) 727–739.

[12] C.L. Folk, R. Remington, and J.C. Johnston, Involuntary covert orienting is contingent on attentional control settings. *J. Exp. Psychol. Hum. Percept. Perform.* 18 (1992) 1030–1044.

[13] D.R. Gitelman and A.C. Nobre, T.B. Parrish, K.S. LaBar, T.H. Kim, J.R. Meyer, and M.M. Mesulam, A large-scale distributed network for covert spatial attention. *Brain* 122 (1999) 1093–1106.

[14] J.P. Gottlieb, M. Kusunoki, M.E. and Goldberg, The representation of visual salience in monkey parietal cortex. *Nature* 391 (1998) 481–484.

[15] D.P. Hanes, K.G. Thompson, and J.D. Schall, Relationship of presaccadic activity in frontal and supplementary eye field to saccade initiation in macaque: Poisson spike train analysis. *Exp. Brain Res.* 103 (1995) 85–96.

[16] W. Heide, F. Binkofski, R.J. Seitz, S. Posse, M.F. Nitschke, H.J. Freund, and D. Kompf, Activation of frontoparietal cortices during memorized triple-step sequences of saccadic eye movements: an fMRI study. *Eur. J. Neurosci.* 13 (2001) 1177–1189.

[17] J.B. Hopfinger, M.H. Buonocore, and G.R. Mangun, The neural mechanism of top-down attentional control. *Nat. Neurosci.* 3 (2000) 284–291.

[18] M.S. Kim and K. Cave, Top-down and bottom-up attentional control: On the nature of interference from a salient distractor. *Percept. Psychophys.* 61 (1999) 1009–1023.

[19] Y.H. Kim, D.R. Gitelman, A.C. Nobre, T.B. Parrish, K.S. LaBar, and M.M. Mesulam, The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *NeuroImage* 9 (1999) 269–277.

[20] S. Kastner, M.A. Pinsk, P. De Weerd, R. Desimone, and L.G. Ungerleider, Increased Activity in Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron* 22 (1999) 751–761.

[21] T. Kumada, Limitation in attending to a feature value for overriding stimulus-driven interference. *Percept. Psychophys.* 61 (1999) 61–79.

[22] M. Kusunoki, J. Gottlieb, and M.E. Goldberg, The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion and task relevance. *Vision Res.* 40 (2000) 1459–1468.

[23] U. Leonards, S. Sunaert, P.V. Hecke, and G.A. Orban, Attentional mechanism in visual search—An fMRI Study. *J. Cogn. Neurosci.* 12 (2000) 61–75.

[24] R.M. Müri, M.T. Iba-Zizen, C. Derosier, E.A. Cabanis, and C. Pierrot-Deseilligny, Location of the human posterior eye field with functional magnetic resonance imaging. *J. Neurol. Neurosurg. Psychiatry* 60 (1996) 445–448.

[25] A.C. Nobre, D.R. Gitelman, E.C. Dias, and M.M. Mesulam, Covert visual spatial orienting and saccades: overlapping neural systems. *NeuroImage* 11 (2000) 210–216.

[26] A.C. Nobre, G.N. Sebestyen, D.R. Gitelman, M.M. Mesulam, R.S. Frackowiak, and C.D. Frith, Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, 3 (1997) 515–533.

[27] R.C. Oldfield, (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1971) 97–113.

[28] S. Pollmann and D.Y. von Cramon, Object working memory and visuospatial processing: functional neuroanatomy analyzed by event-related fMRI. *Exp. Brain Res.* 133 (2000) 12–22.

[29] A.C. Rosen, S.M. Rao, P. Caffarra, A. Scaglioni, J.A. Bobholz, S.J. Woodley, T.A. Hammeke, J.M. Cunningham, T.E. Prieto, and J.R. Binder, Neural basis of endogenous and exogenous spatial orienting: A functional MRI study. *J. Cogn. Neurosci.* 11 (1999) 135–152.

[30] M.F.S. Rushworth, T. Paus, and P.K. Sipila, Attention systems and the organization of the human parietal cortex. *J. Neurosci.* 21 (2001) 5262–5271.

[31] J.D. Schall, D.P. Hanes, K.G. Thompson, and D.J. King, Saccade target selection in frontal eye field of macaque. I. Visual and premovement

activation. *J. Neurosci.* 15 (1995) 6905–6918.

[32] R.I. Schubotz and D.Y. von Cramon, Functional organization of the lateral premotor cortex: fMRI reveals different region activated by anticipation of object properties, location and speed. *Cogn. Brain Res.* 11 (2001) 97–112.

[33] G.L. Shulman, J.M. Ollinger, E. Akbundak, T.E. Conturo, A.Z. Snyder, S.E. Petersen, and M. Corbetta, Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci.* 19 (1999) 9480–9496.

[34] J. Theeuwes, Cross-dimensional perceptual selectivity. *Percept. Psychophys.* 50 (1991) 184–193.

[35] J. Theeuwes, Perceptual selectivity for color and form. *Percept. Psychophys.* 51 (1992) 599–606.

[36] J. Theeuwes, Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Percept. Psychophys.* 20 (1994) 799–806.

[37] K.G. Thompson, D.P. Hanes, N.P. Bichot, and J.D. Schall, Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *J. Neurophysiol.* 76 (1996) 4040–4055.

[38] M. Turatto and G. Galfano, Color, form and luminance capture attention in visual search. *Vision Res.* 40 (2000) 1639–1643.

[39] M. Turatto and G. Galfano, Attention capture by color without relevant attentional set. *Percept. Psychophys.* 63 (2001) 286–297.

[40] E. Wojciulik and N. Kanwisher, The generality of parietal involvement in visual attention. *Neuron* 23 (1999) 747–764.

[41] S. Yantis and H.E. Egger, On the distinction between visual salience and stimulus-driven attentional capture. *J. Exp. Psychol. Hum. Percep. Perform.* 25 (1999) 661–676.

Figure 1. Stimulus displays used in the present study. Blue arrows indicate the target item in each display. 1a: Feature search, set size: 8; 1b: Singleton search, set size: 8, target: diamond. Stimuli 1a and 1b were used in all experiments. 1c: Feature search, set size: 6, used in Exp. 1a. 1d: Feature search, set size: 8, with a distractor, used in Exp. 1b. 1e: Control, used in Exp. 2. 1f: Cue stimuli for the singleton search, used in Exp. 2. A diamond was presented in the feature search and only a fixation cross was presented in the control task as cue stimuli. dist.: distractor.

Figure 2. Activation maps obtained from group analyses. Three different maps were co-interrupted to a normalized structure image of a subject. Cyan-Magenta color map (left color bar): the $(FS + SS) - C$ subtraction; Red-Yellow color map (middle color bar): the $SS - FS$ subtraction; Blue-Green color map (right color bar): the $FS - SS$ subtraction. Each activation map shows the voxel which exceed the height threshold $T = 3.11$ (corresponding to $p < .001$ uncorrected for multiple comparison). Note that not all the voxels revealed here exceeded the extent threshold.

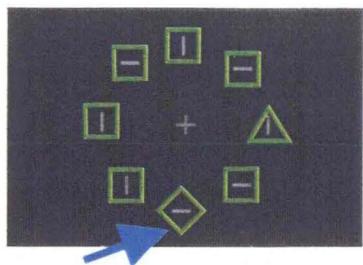
Figure 3. The FEF and the intraparietal activation of a representative single subject. 3a: Activation of the bilateral FEF (left picture) and the bilateral intraparietal area obtained from the individual the $(FS + SS) - C$ subtraction (Cyan-Magenta color map) and the $SS - FS$ subtraction (Red-Yellow color map); height threshold $T = 3.12$, extent threshold $p < .05$ corrected for multiple comparisons. 3b: MR signal time course obtained from a single

subject. The figures in the left column are for session 1, and those in the right column are for the session 2. FS: feature search, SS: singleton search, C: control, FEF: frontal eye field, IPS: intraparietal sulcus.

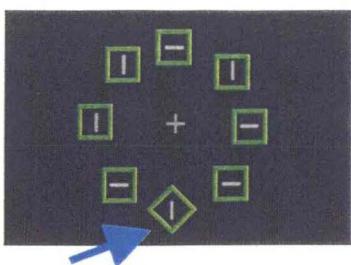
Figure 4. The intraparietal activations obtained from individual analyses of seven subjects. All images showed activations revealed in the $Z = 40$ plane in the MNI coordinates (height threshold $T > 3.12$, inclusively masked by the individual $[FS + SS] - C$ subtraction [$p < .05$ uncorrected for multiple comparisons]).

Figure 1

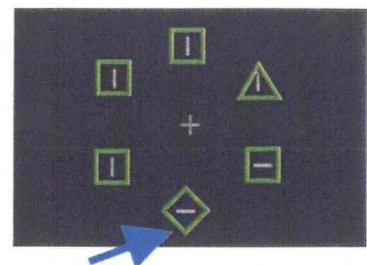
a. FS-8



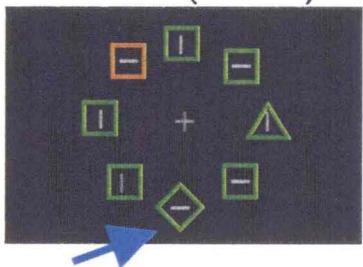
b. SS-8



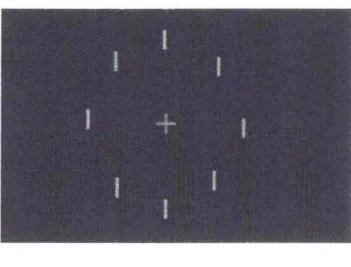
c. FS-6



d. FS-8 (dist.)



e. control



f. cue for SS



Figure 2

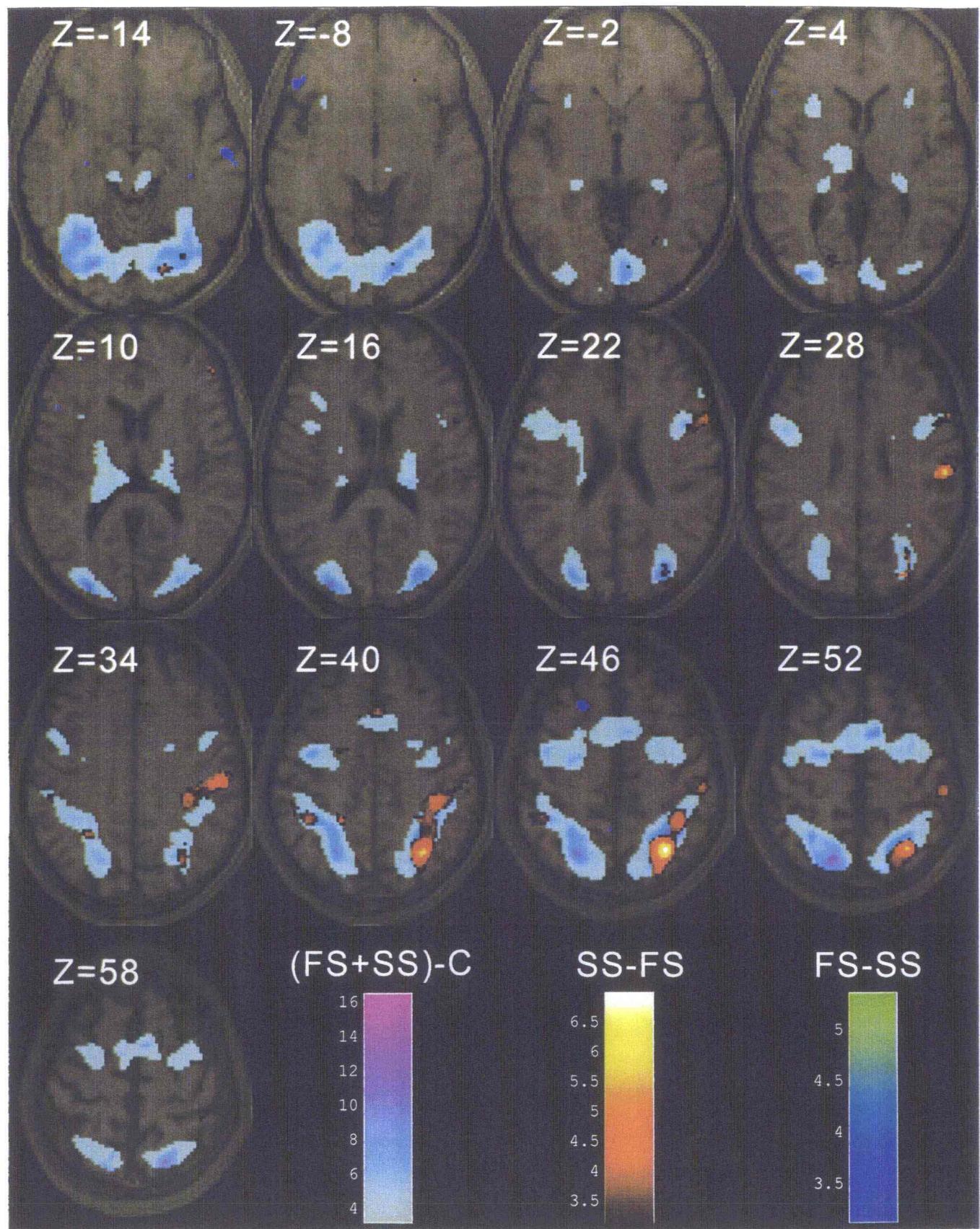


Figure 3

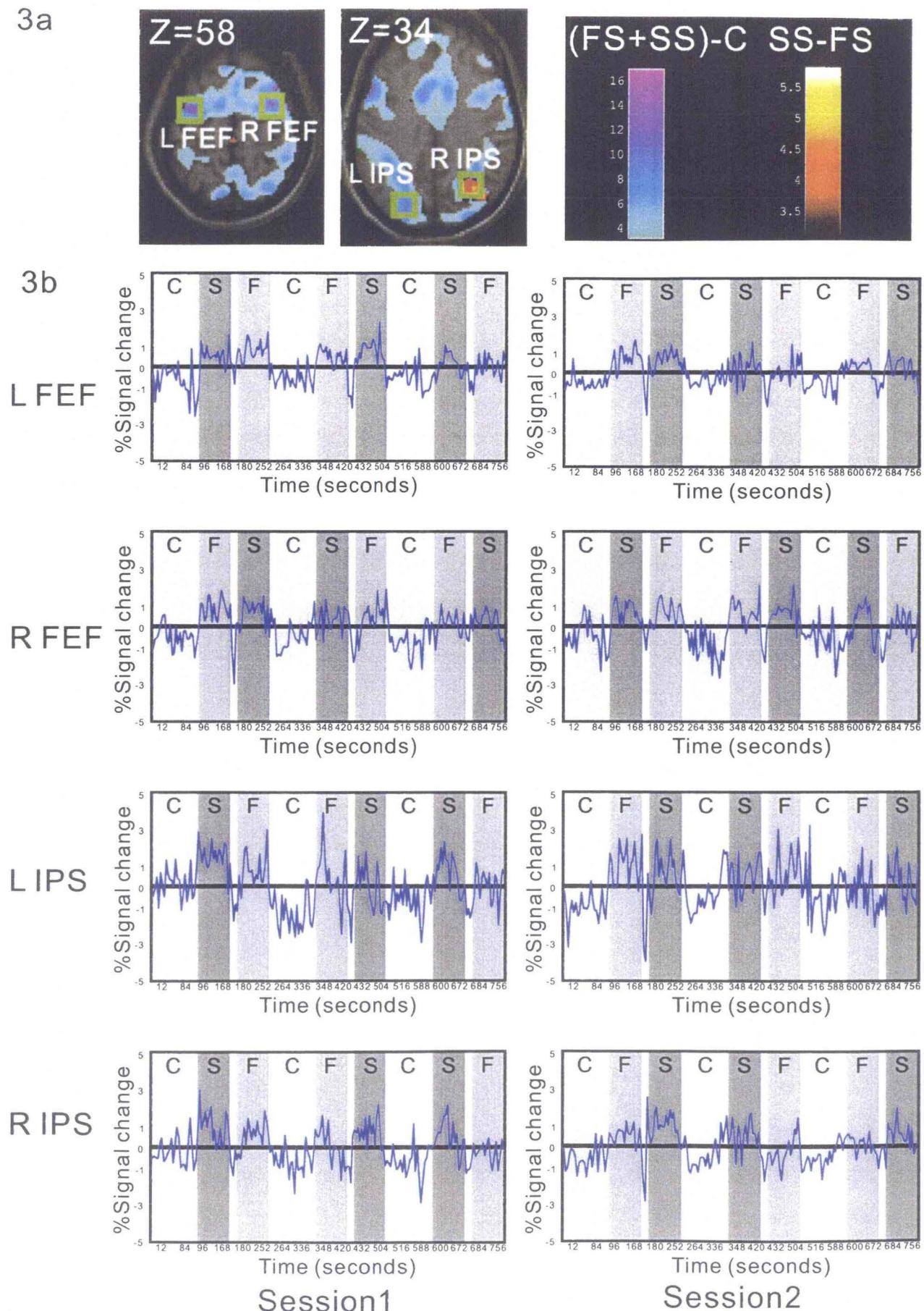


Figure 4

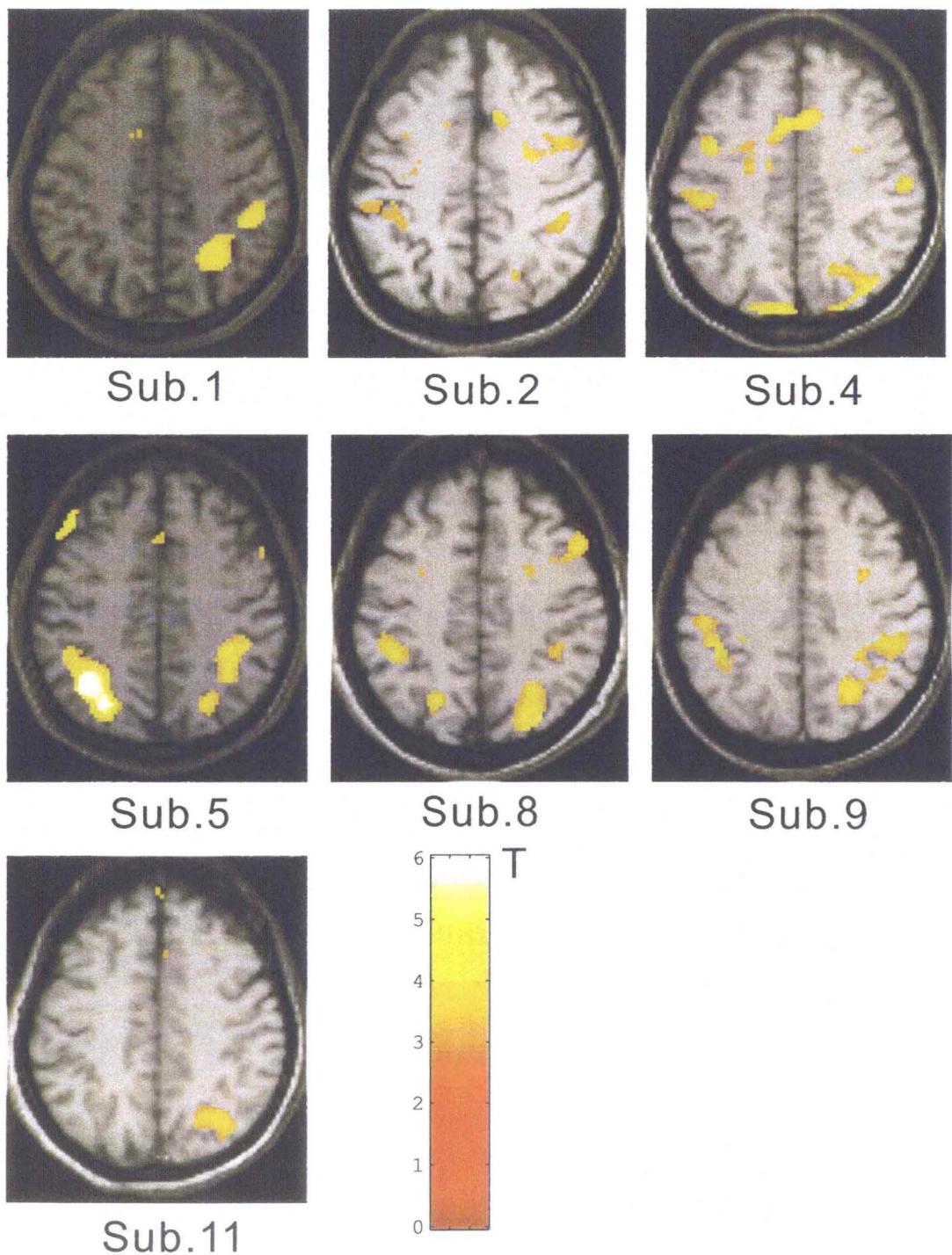


Table 1. Mean Reaction Time, Mean Error Rates, and Mean Saccade Rates for Each Condition in Experiment 1 (in percent).

Exp. 1a			
Feature Search	6	8	10
Reaction Time (S.E.M.)	983.93 (63.77)	1011.48 (54.68)	967.26 (59.52)
Error Rate (S.E.M.)	4.83 (1.62)	4.17 (1.22)	4.83 (1.14)
Saccade Frequency (S.E.M.)	6.17 (2.61)	5.50 (2.08)	9.00 (2.99)
Singleton Search	6	8	10
Reaction Time (S.E.M.)	1031.66 (86.12)	1049.81 (79.68)	1008.38 (100.10)
Error Rate (S.E.M.)	6.5 (0.82)	7.01 (1.14)	4.01 (1.10)
Saccade Frequency (S.E.M.)	5.50 (1.28)	7.17 (2.08)	6.50 (1.81)
Exp. 1b			
Feature Search	Distractor	No Distractor	
Reaction Time (S.E.M.)	987.69 (62.80)	1055.98 (68.44)	
Error Rate (S.E.M.)	5.33 (1.16)	2.68 (2.34)	
Saccade Frequency (S.E.M.)	4.33 (1.80)	7.00 (3.62)	
Singleton Search	Distractor	No Distractor	
Reaction Time (S.E.M.)	1030.23 (92.75)	1187.29 (110.73)	
Error Rate (S.E.M.)	9.00 (1.63)	5.00 (2.38)	
Saccade Frequency (S.E.M.)	6.00 (1.93)	6.33 (1.87)	

Table 2. Mean Reaction Time (in msec) and Mean Error Rates (in percent) for Each Condition in Experiment 2.

	FS		SS		C	
Reaction Time (S.E.M.)	964.34	(33.80)	961.4	(32.37)	520.38	(24.28)
Error Rate (S.E.M.)	5.13	(1.52)	6.29	(0.91)	0.89	(0.36)

FS: Feature Search; SS: Singleton Search, C: Control

Table 3. Coordinates of Activated Regions Obtained from Group Analyses

Region		Coordinates (x, y, z) t value							
		Singleton – Feature			(Singleton + Feature) – Control				
	ACC				10	8	50	9.45	
	SMA				-8	-2	56	5.42	
L	FEF				-26	0	62	4.97	
R	FEF				32	-2	52	5.62	
L	vPM				-38	6	18	5.86	
L	pCG				-56	-28	34	3.84	
R	pCG	56	-22	30	6.04				
L	AIPS				-48	-36	44	4.97	
R	AIPS	38	-34	38	5.16	46	-34	40	5.31
L	IPS				-28	-52	42	9.10	
R	IPS	40	-46	44	4.56	34	-50	44	10.42
L	PIPS				-26	-64	44	10.88	
R	PIPS	32	-64	46	6.99	26	-70	46	9.02
L	Precuneus				-18	-70	54	12.79	
R	Precuneus				18	-68	60	13.40	
L	IPTO				-30	-90	14	16.44	
R	IPTO				28	-84	20	10.24	
L	FG				-36	-80	-20	10.53	
R	FG				36	-72	-18	9.35	
R	LG				14	-82	-10	8.18	
L	LG				-12	-86	-10	6.87	
L	Pulvinar				-20	-32	10	4.99	
R	Pulvinar				24	-26	16	5.38	

ACC: anterior cingulate cortex, FEF: frontal eye field, vPM: ventral premotor area, pCG: post central gyrus, AIPS: anterior part of intraparietal sulcus, PIPS: posterior part of IPS, IPTO: junction of IPS and transverse occipital sulcus, FG: fusiform gyrus, LG: lingual gyrus