Transient neural activity in human parietal cortex during spatial attention shifts

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Observers viewing a complex visual scene selectively attend to relevant locations or objects and ignore irrelevant ones. Selective attention to an object enhances its neural representation in extrastriate cortex, compared with those of unattended objects, via top-down attentional control signals. The posterior parietal cortex is centrally involved in this control of spatial attention. We examined brain activity during attention shifts using rapid, event-related fMRI of human observers as they covertly shifted attention between two peripheral spatial locations. Activation in extrastriate cortex increased after a shift of attention to the contralateral visual field and remained high during sustained contralateral attention. The time course of activity was substantially different in posterior parietal cortex, where transient increases in activation accompanied shifts of attention in either direction. This result suggests that activation of the parietal cortex is associated with a discrete signal to shift spatial attention, and is not the source of a signal to continuously maintain the current attentive state.

Natural scenes contain more information than the human visual system can efficiently process at once. Visual attention is the perceptual mechanism by which observers select important aspects of a scene for further cognitive processing[1–5]. Evidence from neurophysiology and functional neuroimaging shows that the neural representation of a visual object is suppressed when it is presented along with other competing objects, relative to when it is presented alone, reflecting competitive interactions among sensory representations. This competitive suppression is thought to occur through inhibitory neural connections. When an object is attended through the action of a top-down biasing signal, this suppression is effectively lifted, and the item is 'selected'[6–8].

Investigations of the neural basis of visual attention have focused on two distinct aspects of this mechanism: the effect of attentional modulation in early sensory cortex[6–18] and the source of the attentional control signal in parietal and frontal cortex[19–33]. Evidence from the unilateral neglect syndrome, from neurophysiological studies in animals, and from functional neuroimaging studies in humans have implicated the posterior parietal lobe in particular as a center for controlling the deployment of attention to locations in space. What is less clear is its precise function in attentional control.

At least two different possibilities must be considered. According to the 'sustained hypothesis', activity in the parietal lobes provides a continuous signal that maintains the locus of attention at a spatial location by biasing competition in lower visual areas or by acting as a gate that permits only relevant information to be passed from early visual cortex to ventral stream areas (for example, inferotemporal cortex) for object recognition. This hypothesis predicts sustained increases in neural activity in both extrastriate (attentionally modulated) areas and parietal (attentional control) areas when attention is directed to a location in space for an extended period of time. Furthermore, shifts in attention should give rise to parallel changes in activity in these two areas.

An alternative hypothesis is that activity in the parietal lobes may be specifically related to the act of shifting attention from one location to another. This 'transient hypothesis' contends that the parietal lobes may be the source of a brief attentional control signal to shift attentive states, but not a source of a continuous signal to actively maintain the new state. The locus of attention could be maintained by some other (cortical or subcortical[34–36]) area that serves as a 'latch'[37,38], or by a self-excitatory positive feedback mechanism that maintains attention until a new shift signal arrives. Regardless of the mechanism by which attention
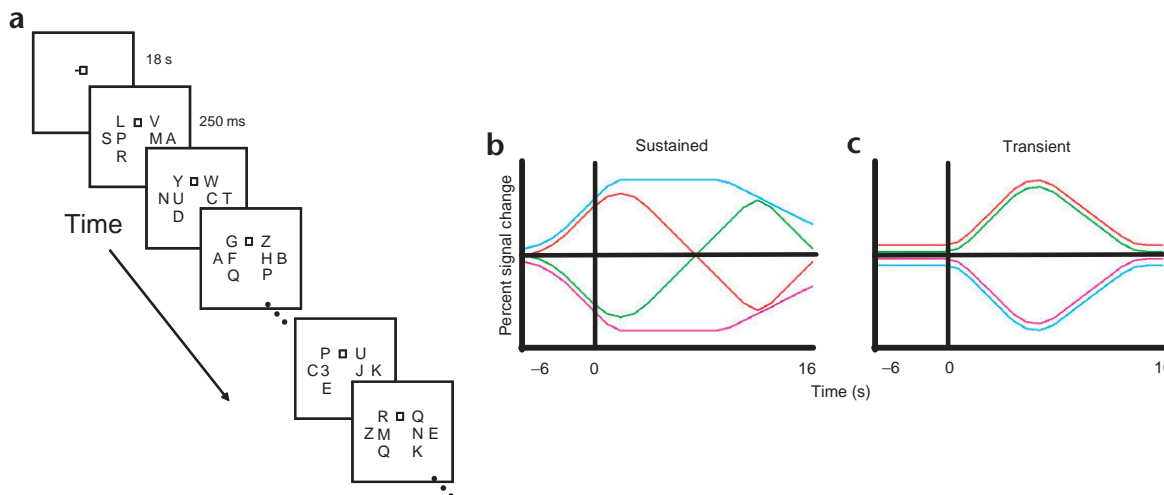
Fig. 1. Task and predictions. (**a**) The rapid serial visual presentation (RSVP) task. Participants were asked to fixate on the central square throughout each run in the scanner. An attention cue indicating whether the right or left side should initially be attended appeared for 18 s at the beginning of each run and then disappeared. Each of eight RSVP streams consisted of letters appearing in random order, one after another, in the same spatial location. They changed synchronously every 250 ms with no temporal gap. Two target streams (one on each side) were each surrounded by three distractor streams. Digits appeared within the target RSVP stream on the attended side, separated by 3–5 s. The task was to press buttons held in both hands whenever a digit was detected, and to either maintain attention on the same side (for hold targets) or shift attention to the other side (for shift targets). The target digits were 3 and 7, mapped to hold and shift, respectively, for half the participants and the reverse mapping for the other half. (**b**, **c**) Hypothetical event-related BOLD time courses illustrating the sustained and transient accounts of attentional control. (**b**) The pattern of activity expected from an area that mirrors or maintains the current locus of attention according to the sustained account. Increased relative activity following a hold event on the contralateral side of space (cyan) contrasts with the reduced activity evoked by a hold event on the ipsilateral side of space (magenta). Activity after the shift events yields a crossover pattern: a shift from the ipsilateral to the contralateral side leads to an increase in activity (green), and a shift from the contralateral to the ipsilateral side of space leads to a decrease in activity (red). This area is characterized by a main effect of target location (left or right). The attentional modulation is evident at time 0 because attention is already deployed to the target location at that moment as a result of previous target events. Activation approaches 0% signal change near the beginning and end of the time course because here the BOLD signal of the randomly selected preceding and following events tend to cancel each other out. (**c**) The pattern of activity from an area that issues a transient signal when attention is shifted to either side of space. This area is defined by a main effect of target type (shift versus hold) in the absence of an effect of target location that defines the pattern in (**b**). The transient hypothesis does not make a precise prediction about the time course of activity after hold targets.

is maintained, this hypothesis predicts a transient increase in shift-related parietal activation that is not sustained during periods of focused attention.

Here we used rapid, event-related functional magnetic resonance imaging (fMRI) to examine the unique temporal signature of the blood oxygenation level–dependent (BOLD) signal predicted by these two accounts. The sustained and transient hypotheses of parietal function differ in the predicted time course of neural activity, and not in the predicted spatial distribution of cortical activity, during attention shifting. Our results clearly favor the transient hypothesis.
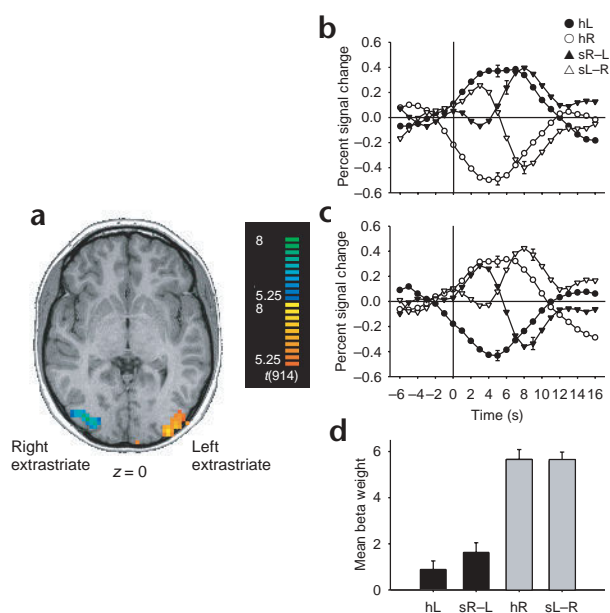
RESULTS

We investigated the role of the parietal lobes in controlling the locus of attention by modifying a previously described perceptual task[39,40] (**Fig. 1a** and Methods), which has several advantages over other methods. The inclusion of multiple nearby distractor items maximizes the degree of sensory competition and therefore enhances attentional modulation[1,6–8]. The visual stimulus, motor requirements and state of focused attention are constant at all times; only the attentional shifts required by shift targets are manipulated. The rapid serial visual presentation (RSVP) streams constitute a steady-state visual stimulus that avoids sensory events such as a discrete attentional cue or a discrete target that would evoke a wave of primary sensory activity,

thereby interfering with measurements of the purely top-down attentional effects of interest.

There are two different idealized patterns of event-related time courses corresponding to the predicted patterns for the sustained (**Fig. 1b**) and transient (**Fig. 1c**) hypotheses. In **Fig. 1b**, activation is greater when attention is maintained on the contralateral side of space (cyan) versus the ipsilateral side (magenta); shifts of attention from the contralateral to the ipsilateral side or viceversa (red or green) yield a crossover pattern. This pattern would be expected from attentionally modulated regions of extrastriate cortex, and have been observed in physiological studies in monkeys[10]. Similar patterns would be expected from an attentional control area that continuously modulates extrastriate cortex, as predicted by the sustained hypothesis. Note that when, for example, a hold target appears in the contralateral RSVP stream at time 0 (the moment when the shift or hold target occurs), the subject's attention has already been directed to that location as a result of previous hold-contralateral or shift-to-contralateral targets. Thus, an effect of contralateral versus ipsilateral attention is expected at time 0.

A different pattern is expected from an attentional control area that shows transient activity when attention is shifted between spatial locations, independent of the direction of the shift (**Fig. 1c**). The transient nature of the shift-related activity is manifested in two features of this pattern. First, there is no dif-

Fig. 2. Pattern of activation for a single participant resulting from a contrast specifying that the hold-contralateral and the shift-to-contralateral beta weights were greater than the hold-ipsilateral and the shift-to-ipsilateral beta weights. (**a**) One transverse slice reveals clusters of activation in right (blue-green) and left (red-orange) extrastriate cortex. The scale at right shows the value of the obtained *t* statistic (Bonferroni corrected, *P* < 0.01). Associated with each activated cluster is the mean event-related average time course of the BOLD signal for each of four event types: (**b**) The event-related time course of activity from the cluster of activated voxels in right extrastriate cortex. (**c**) The time course of activity from the cluster of activated voxels in left extrastriate cortex. (**d**) The mean beta weights from the cluster of significantly activated voxels in left extrastriate cortex showing the main effect of target location. Talairach coordinates[46] of the centers of mass for each activation (*x, y, z*): right extrastriate (28, −77, 2), left extrastriate (−29, −81, 1). Hold-left (hL, closed circle), shift-right-to-left (sR–L, closed triangle), hold-right (hR, open circle) and shift-left-to-right (sL–R, open triangle). Error bars, ± s.e.m.

tinuously maintains the current state of attention, and that is not lateralized, then one would expect no event-related effects at all. Such an area would be continuously active throughout our task because attention was always directed to locations away from fixation, and would therefore be undetectable.

Contralateral attentional modulation

We identified areas that exhibited the crossover pattern (**Fig. 1b**) using a general linear model (GLM) to contrast regressors for hold-contralateral and shift-to-contralateral target events versus hold-ipsilateral and shift-to-ipsilateral target events. We determined the spatial pattern of activation in right and left extrastriate areas (**Fig. 2a**, data from one representative subject) and the mean event-related time course of the BOLD signal from the significantly activated cluster of voxels in right (**Fig. 2b**) and left (**Fig. 2c**) extrastriate

ference between the attend-contralateral and attend-ipsilateral conditions at time 0 (compare **Fig. 1b** and **c**). One would expect such a difference only in a region that was continuously maintaining the current state of attention. Second, the 'shift' time courses (red and green) depart uniformly from the 'hold' time courses (cyan and magenta) a few seconds after the target events occur. This reflects the fact that this region issues a transient signal that is specifically time-locked to shift events. An area that either reflects the current locus of attention or that is the source of a signal that continuously maintains the current attentive state should exhibit the crossover pattern in **Fig. 1b**; an area that generates discrete signals to redirect attention to either side of space should exhibit the pattern in **Fig. 1c**.

A third alternative can also be considered. If there exists an attentional control center that con-

Fig. 3. Group random-effects analysis examining the consequences of directing attention to the left and right target streams. (**a**) Significant group activation in right and left extrastriate cortex, identified using a contrast specifying that the hold-contralateral and the shift-to-contralateral beta weights were greater than the hold-ipsilateral and the shift-to-ipsilateral beta weights. (**b**) Group activation in left ventral IPS. (**c**) Mean group beta weights from the active cluster in right extrastriate cortex (31, −74, 5), revealing increased activation when attention is directed to the left side of space. (**d**) Mean group beta weights from the active cluster in left extrastriate cortex (−35, −74, 2) showing increased activation when attention is directed to the right side of space. (**e**) Mean group beta weights from left IPS (−19, −72, 33), showing that this area is more active when attention is directed to the right side of space. (**f–h**) Mean event-related BOLD time courses from right and left extrastriate and left IPS, respectively. Hold-left (hL, closed circle), shift-right-to-left (sR–L, closed triangle), hold-right (hR, open circle) and shift-left-to-right (sL–R, open triangle). Error bars, ± s.e.m.
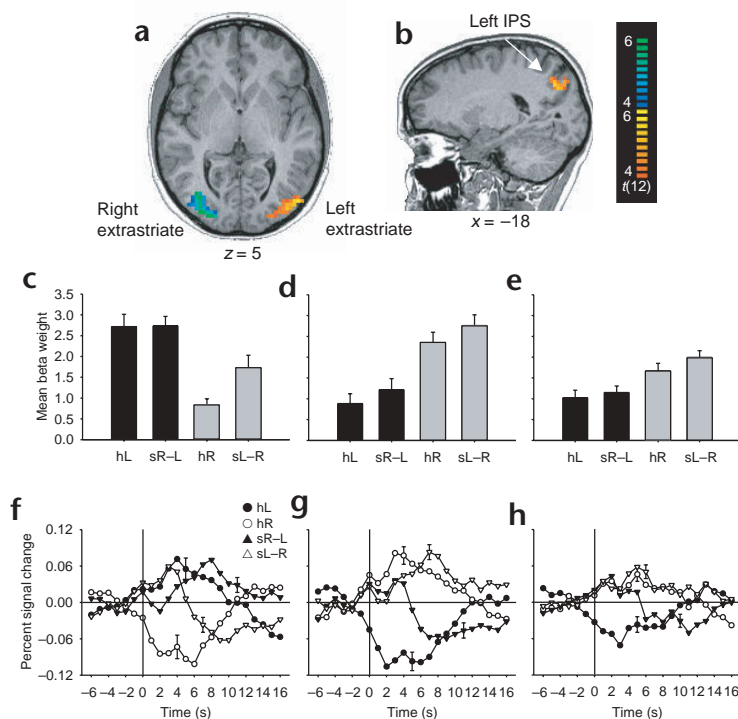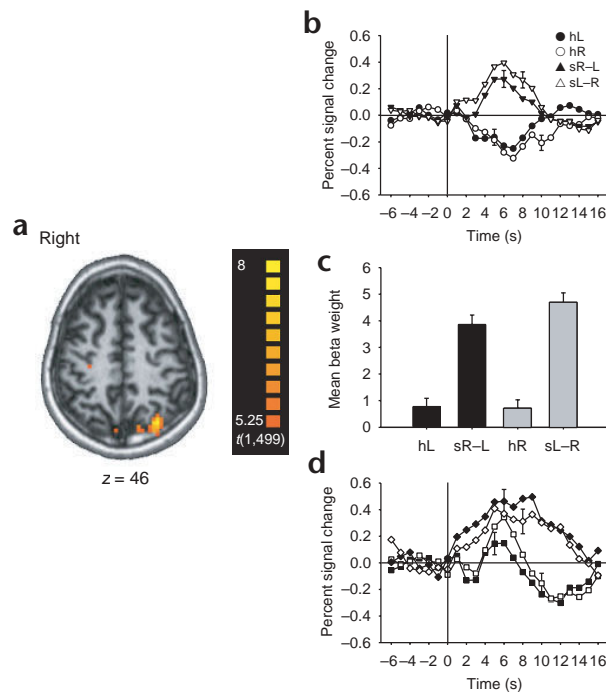
Fig. 4. Pattern of activation from a single participant identified with a contrast between the shift and hold beta weights. (**a**) A transverse slice through parietal cortex reveals activation in left SPL (–27, –65, 46). (**b**) The event-related time course of activity from the cluster of activated voxels in the left SPL; hold-left (hL, closed circle), shift-right-to-left (sR–L, closed triangle), hold-right (hR, open circle) and shift-left-to-right (sL–R, open triangle). (**c**) The mean beta weights from the cluster of voxels in left SPL showing a main effect of shifting attention and no interaction between location and attention cue type. (**d**) The time course of activity time-locked to shift events that are followed by another shift event (shift-right-to-left, open diamond; shift-left-to-right, closed diamond) and that are followed by two hold events (sR–L, open square; sL–R, closed square). Error bars, ± s.e.m.

cortex, for each of the four event types: hold-left (hL), shift right-to-left (sR–L), hold-right (hR) and shift left-to-right (sL–R). Each time course is the mean of approximately 70 events (misses were excluded from the analysis) and is time-locked to the target event in question. The baseline for each of the event types was the mean BOLD signal for the 6 s preceding that event.

The effects of sustained spatial attention can be seen by comparing the time course for hL (filled circles) and hR (open circles) target events in extrastriate cortex (**Fig. 2b** and **c**): the BOLD signal was greater when attention was directed to the contralateral side of the visual field than when it was directed to the ipsilateral side. As noted earlier, the BOLD signal is already different for hR and hL targets when the target event occurs (time 0); this is because attention had been directed to the target location by a previous target event. The BOLD signal remained relatively strong (contralateral attention) or relatively weak (ipsilateral attention) for several seconds after a hold target was presented.

We observed a different pattern following shift targets. The time course in right extrastriate cortex for sL–R targets began by closely following the hL time course, but decreased toward the hR time course after the shift target appeared (**Fig. 2b**). The opposite pattern was found for sR–L targets. The complementary pattern was observed in left extrastriate cortex (**Fig. 2c**).

The mean beta weights estimated by GLM analysis for each of the four regressors from the activated cluster of voxels in left extrastriate cortex (**Fig. 2d**) demonstrate a main effect of target location ([hR and sL–R] > [hL and sR–L]) that produced the crossover pattern in **Fig. 2c**.

We used a random-effects, group GLM to identify cortical areas that were more active across all 13 participants when attention was directed to the right rather than to the left target stream, and vice-versa (**Fig. 3a** and **b**). This analysis contrasted hL and sR–L regressors with hR and sL–R regressors. A main effect of target location was evident in both left and right extrastriate cortex (**Fig. 3c** and **d**) such that activity was greater when attention was shifted to or maintained in the contralateral versus the ipsi-

lateral visual field. An area in left ventral intraparietal sulcus (vIPS, **Fig. 3e**) also showed a main effect of target location, with greater activation when attention was directed to the contralateral (right) side of space. We also determined the group mean event-related time courses from the right and left extrastriate and left IPS activations (**Fig. 3f–h**).

Shift-related activity
We contrasted shift and hold events to identify any regions that showed transient shift-related activity (**Fig. 1c**). We found that the BOLD time course in the superior parietal lobule (SPL, see **Fig. 4a** and **b** for data from a representative subject) contrasted sharply with that observed in extrastriate cortex (**Fig. 2b** and **c**). First, there was no difference in SPL activity for attend-left and attend-right events at time 0, indicating that SPL does not continuously maintain a location-specific attentive state throughout the task. After a sL–R or a sR–L target event, there was an increase in the BOLD signal; hL and hR events resulted in a significantly smaller BOLD signal. **Figure 4c** shows the main effect of target type (shift versus hold) as reflected in the beta weights for this analysis. Note that although the shift beta weights were much greater than the hold beta weights, all regressors were significantly greater than zero (hL, $t_{(1,499)} = 2.5$, $P < 0.05$; hR, $t_{(1,499)} = 2.35$, $P < 0.05$; sR–L, $t_{(1,499)} = 10.9$, $P < 0.0001$; sL–R, $t_{(1,499)} = 13.3$, $P < 0.0001$). This finding is elaborated in the Discussion.

Eight of the subjects participated in a task variant in which hold targets always appeared in pairs. Thus, a shift event could be followed either by another shift event or by two consecutive hold events. The transient hypothesis predicts prolonged activity for a shift followed by another shift, compared to the activity produced by a shift followed by two hold events. The latter case should lead to an initial increase in activity, followed by a sustained decrease in activity while attention was maintained at the newly attended location. **Figure 4d** shows the time course of activity from SPL broken down by this factor for the single subject depicted in **Fig. 4a**. Activity after a shift target increased and remained high if it was immediately followed by another shift target. In contrast, activity initially increased and then declined rapidly when a shift event was followed by two successive hold events. This pattern strongly supports the transient hypothesis.

A random effects contrast specifying a main effect of shifting attention was also performed on the group data. This contrast identified activation in right SPL, right inferior parietal lobule (IPL), right inferior temporal gyrus (ITG, near the occipital extension of the inferior temporal sulcus, perhaps V5), right precentral gyrus (preCG), left anterior thalamus region (AT), left pulvinar and the left inferior frontal sulcus (IFS) (**Table 1**).

Testing for a main effect of shifting attention will identify regions that are transiently active during attention shifts; how-

Table 1. Brain regions exhibiting greater activation for shifting than holding attention.
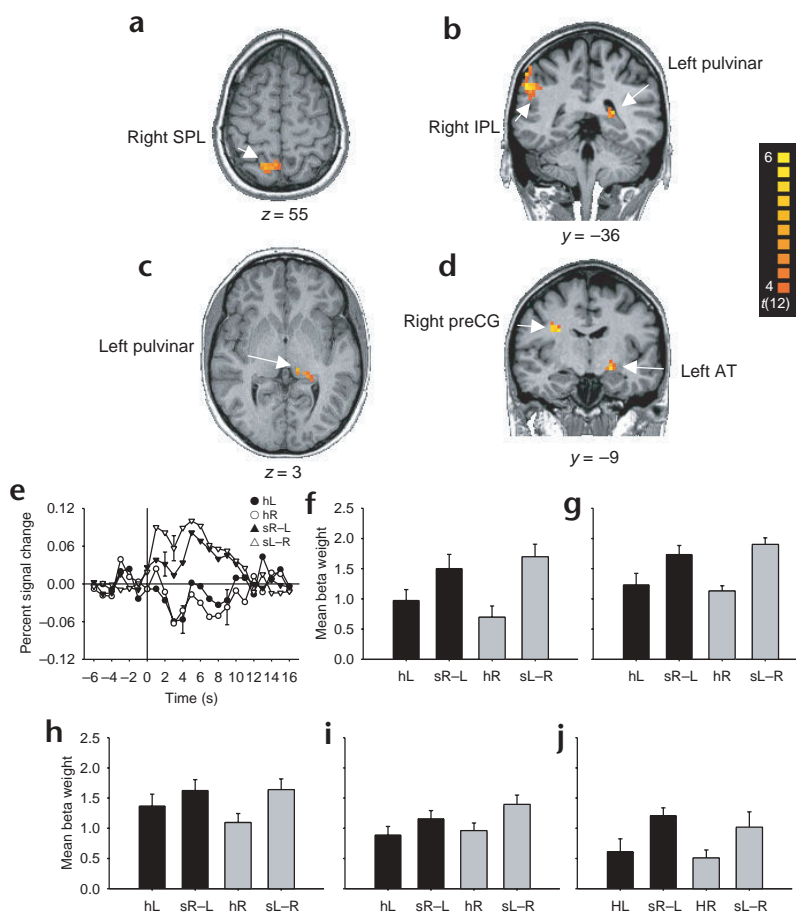
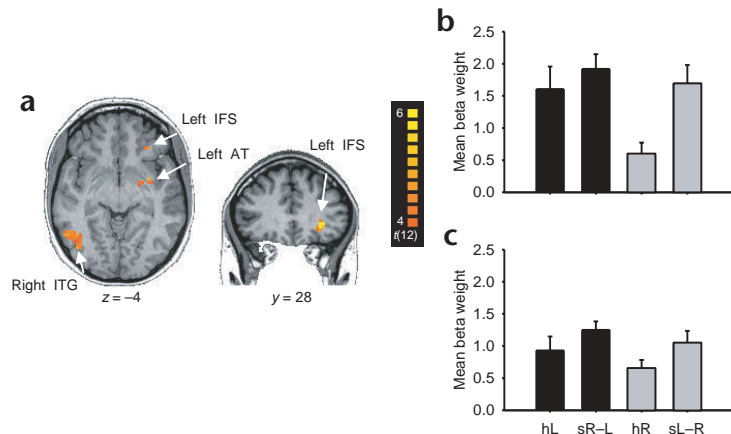| Area	Side	Size (ml)	Talairach coordinates	Main effect: shift versus hold $F_{(1,12)}$	Main effect: L versus R $F_{(1,12)}$	Interaction $F_{(1,12)}$
Superior parietal lobule	Right	0.918	11, −60, 55	32.5*, $P < 0.001$	0.1	1.9
Inferior parietal lobule	Right	1.890	46, −31, 28	46.3*, $P < 0.001$	0.01	1.4
Precentral gyrus	Right	0.540	29, −5, 26	48.4*, $P < 0.001$	0.6	3.0
Pulvinar	Left	0.540	−14, −31, 4	74.0*, $P < 0.001$	1.9	0.36
Anterior thalamus	Left	1.215	−20, −1, −6	52.7*, $P < 0.001$	1.6	0.08
Inferior temporal gyrus	Right	1.431	44, −57, −3	31.4*, $P < 0.001$	14.6*, $P < 0.005$	5.5*, $P < 0.05$
Inferior frontal sulcus	Left	0.459	−27, 28, 2	50.1*, $P < 0.001$	7.7*, $P < 0.05$	0.13

*Significant F value.

ever, areas that exhibit a main effect of both left versus right and shift versus hold will not be excluded. In an effort to restrict our analysis to areas that exhibited a 'pure' shift pattern (as in **Fig. 1c**), we conducted two-way repeated measures ANOVA on the beta weights from each of the activated shift versus hold regions to assess possible main effects of location. A main effect of target type (shift versus hold) in the absence of a main effect of location indicates that an area mediates shifts of attention without a preference for one visual field over the other; this is the signature of a 'pure' transient shift region. In contrast, a main effect of shifting attention coupled with a main effect of location reflects an area whose shift-related activity may differ for the two sides of space (for example, an area that exhibits the crossover pattern of activity evident in **Figs. 2** and **3**, but is nevertheless more active on average after a shift than it is after a hold event, would fall into this category).

The pattern of activation resulting from the group random-effects GLM and the corresponding beta weights from each of the activated areas showed a main effect of shifting attention (**Figs. 5** and **6**). Regions of the right SPL, right IPL, right preCG, left AT, and left pulvinar showed a main effect of shifting attention without a preference for location

(**Fig. 5**). The mean event-related BOLD time course for the group from right SPL (**Fig. 5e**) reveals a pattern similar to that seen in **Fig. 4b**. As in the single-subject data reported in **Fig. 5c**, all shift and hold beta weights in each area were significantly greater than zero. Some activations in right ITG and left IFS yielded both a main effect of stimulus type (shift versus hold) and a main effect for location (right ITG, $F_{(1,12)} = 14.6$, $P < 0.005$; left IFS, $F_{(1,12)} = 7.7$, $P < 0.05$; **Fig. 6**). Activity after hL events and sR–L events was greater than activity after hR events and sL–R events in these areas. The significant main effect of location suggests that these two areas may mirror the current locus of attention.

Fig. 5. Significant group activations from regions identified by contrasting shift and hold events in a group random effects GLM. (**a**) A transverse slice through parietal cortex showing an activated region of right SPL. (**b**) A coronal slice through the posterior thalamus, showing activation foci in the left pulvinar and the right IPL. (**c**) A transverse slice through the thalamus showing activation in the left pulvinar. (**d**) A coronal slice through the anterior thalamus showing activation foci in the right preCG and the left anterior thalamus region. (**e**) Mean event-related time course for the group from right SPL. (**f–j**) The bar graphs show the mean beta weights from each of the regions depicted. Separate ANOVAs on the beta weights from each area revealed a significant main effect of shifting attention and no main effect of location. Hold-left, (hL, closed circle), shift-right-to-left (sR–L, closed triangle), hold-right (hR, open circle) and shift-left-to-right (sL–R, open triangle). Error bars, ± s.e.m.

a

b

c

Fig. 6. (**a**) Areas in right ITG and left IFS that exhibited a main effect of shifting attention and a main effect of location. (**b**, **c**) Mean beta weights from the right ITG and the left IFS showing both a main effect of shifting attention and a main effect of location. A significant interaction between target type and location was also evident in the right ITG.

Finally, we examined whether the event-related BOLD time course for the group of eight subjects that experienced paired hold events exhibited the transient pattern seen in **Fig. 4d**. A random-effects GLM was applied to this group and a contrast of shift versus hold revealed a cluster of activated voxels in right SPL (**Fig. 7a**). The mean event-related average for the group following shift events is shown in **Fig. 7b**. As in the single-subject time course depicted in **Fig. 4d**, activity after a shift target remained high when it was followed by another shift target. In contrast, activity declined more rapidly when a shift event was followed by two successive hold targets. A repeated-measures ANOVA was applied to the mean BOLD time course within the significantly activated SPL voxels, restricted to time points 7–11 s after the shift event. This analysis revealed a significant difference within this temporal interval between the shift-shift sequence (diamonds in **Fig. 7b**) and the shift-hold-hold sequence (squares in **Fig. 7b**) ($F_{(1,7)} = 8.23$, $P < 0.05$). This outcome provides further support for the transient hypothesis.

DISCUSSION

The crossover that we observed in extrastriate cortex between the two shift time courses (**Fig. 2b** and **c**) is similar to a previously reported[10] pattern of neural activity. In that study, single-cell recordings were made from area V4 of macaque monkeys while they shifted attention between a stimulus inside the cell's receptive field (RF) and one outside the RF. The mean spiking rate was higher while attending to the stimulus in the RF, and it changed continuously from high to low (or vice-versa) over approximately a 300-ms interval after the shift signal.

The quite different time course of the BOLD signal in the right superior and inferior parietal lobe indicates that subregions of parietal cortex are transiently active when attention shifts between spatial locations. This result supports the transient hypothesis of attentional control in these areas of the parietal lobe. We also found a location-specific pattern of activity in the left poste-

rior IPS (**Fig. 3a**). This area has been previously implicated in attentional control[32]; our results suggest that it may be involved in continuously maintaining the current state of attention. Thus, we suggest that different subregions of parietal cortex may mediate distinct aspects of the control of spatial attention. These data do not allow us to rule out the alternative hypothesis, however, that the parietal lobes are a recipient of attention-related changes in extrastriate areas and transiently prepare for an action (such as an eye movement or a reach) whenever a shift of attention occurs, thereby mediating communication between the visual and motor systems[41]. However, our conclusion that this area is a source of attentional control is bolstered by other evidence for the role of the posterior parietal cortex in controlling shifts of attention[24–33].

One feature of the transient activation time course (**Fig. 4b**) is that the BOLD signal increases after shift targets, but decreases (relative to baseline) after hold targets. One might ask whether this relative decrease in activation represents inhibition of a 'shift center' when attention must be maintained. Because baseline in these time course plots is merely the mean of the signal in the six seconds preceding the target event, and not some special baseline state, this question cannot be answered definitively from the BOLD time course alone.

To address this question, one can consider three possible BOLD time courses that might be reflected in the observed event-related averages. In all three cases, a shift target evokes a positive BOLD response. In case 1, a hold target evokes a decrease in activity. In case 2, there is no response to a hold target. In case 3, a hold target evokes a positive, but small, change in activity.

Each of these cases corresponds to a unique pattern of estimated beta weights from the GLM analysis. All three cases would yield positive beta weights for the two shift regressors. They differ in the magnitude of the beta weights associated with the two hold regressors: case 1 would produce negative beta weights, case 2 would produce beta weights near zero and case 3 would produce positive (but small) beta weights.

Only the last of these patterns was observed in our data (**Figs. 4** and **5**). We therefore conclude that these shift-related areas are not suppressed after hold targets, but instead exhibit an attenuated positive response relative to the BOLD signal that is present during the task when no targets are present. We tenta-

Fig. 7. Pattern of activation from a subset of eight subjects who participated in the run-length version of the paradigm (Methods). (**a**) A transverse slice through parietal cortex showing an area of right SPL that was more active following shift events compared to hold events (15,–58, 58). (**b**) The mean group time course of activity time-locked to shift events that are followed by another shift event (shift-right-to-left, open diamond; shift-left-to-right, closed diamond) and that are followed by two hold events (shift-right-to-left, open square; shift-left-to-right, closed square). Error bars, ± s.e.m.

a

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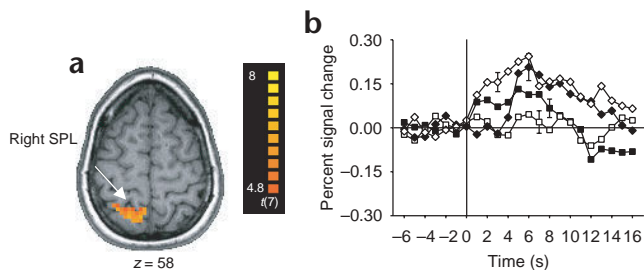
tively speculate that the slight positive response to hold targets shows that these areas may 'refocus' attention at the currently attended location in response to a hold target.

We did not observe extensive shift-related activity in prefrontal cortex as have several other studies[3–5]. One difference between the present paradigm and most previous ones is that participants here were always in a state of focused attention away from fixation (or actively shifting attention), whereas most previous studies used trial-based paradigms in which participants alternated between attending at fixation and attending away from fixation. It is possible that prefrontal cortex is active whenever attention must be disengaged from fixation. Detecting prefrontal activity, therefore, may require a direct contrast of these two attentive states.

Previous studies of attentional control have shown that the parietal lobes are activated during spatial attention tasks[26–33]. The present analysis of event-related time courses in SPL and IPL indicates that sub-regions of parietal cortex do not provide a tonic signal to maintain attention at nonfoveal locations. Instead, the transient activity observed in these areas is tied specifically to the act of shifting attention as postulated nearly two decades ago[25]. Our data indicate that this region is transiently active for shifts both to and from the contralateral hemifield. Whether non-spatial shifts of visual attention are similarly controlled remains an open question.

METHODS

Participants. Fourteen neurologically intact adults (eight females, 23–34 years old) participated in the study. Nine of the subjects (six female) were tested at F. M. Kirby Research Center for Functional Brain Imaging in Baltimore, Maryland; the other five subjects (two female) were tested at the F.C. Donders Centre for Cognitive Neuroimaging in Nijmegen, The Netherlands. Three of the authors (J.S., J.T.S., R.L.C.) served as participants. Data from one of the subjects were discarded because their mean accuracy on the behavioral task was less than 70%, more than two standard deviations below the group mean.

The study protocol was approved by the JHU Joint Committee on Clinical Investigations IRB, and informed consent was obtained from all participants.

Behavioral task. All visual stimuli were rendered in white on a black background. Subjects were instructed to maintain visual fixation on a central box (subtending 0.25° visual angle from a viewing distance of 63 cm). At the beginning of a run, a small tick mark appeared to one side of the fixation box for 18 s, instructing subjects to start with attention directed to the indicated side (**Fig. 1a**). After the tick mark disappeared, eight character streams appeared, with each character simultaneously changing identity every 250 ms. Most of the characters were letters ('A', 'C', 'F', 'G', 'H', 'J', 'K', 'M', 'N', 'P', 'R', 'T', 'U', 'V', 'X' and 'Y' were used), and each letter subtended approximately 0.65° horizontally and 0.8° vertically. The target streams were located 1.45° below the horizontal midline and 1.65° to the left and right of fixation. Each target stream was surrounded on three sides by distractor letter streams with an edge-to-edge separation of 0.25°.

The subjects' task was to detect the digits '3' or '7' that appeared within the target streams. Subjects were instructed to make a button press with the thumbs of both hands every time any target was detected. For half the subjects, the digit '3' instructed the subjects to maintain attention at the currently attended location, while a '7' instructed them to shift attention to the currently unattended target stream. This mapping was reversed for the remaining subjects. The order of events was random for five of the subjects with the constraint that targets could only occur in the attended stream. For the remaining eight subjects (three from Baltimore and five from Nijmegen), hold events always occurred in pairs.

Each run in the scanner lasted for 168 s. For five of the subjects, the number of target events varied slightly between runs, and the targets were separated in time randomly by 3–5 s, and each stimulus presentation sequence lasted for 130 s. Pseudo-random temporal 'jittering' was used so that individual event-related BOLD time courses could be extracted[42,43].

For the remaining subjects, exactly eight instances of each target type occurred in each run and the inter-target interval was uniformly distributed between 3–5 s (at 250-ms intervals). Accuracy in the scanner was 91 ± 3%, 92 ± 2%, 93 ± 2% and 94 ± 1% for hL, hR, sL–R and sR–L targets, respectively. Planned pairwise *t*-tests revealed no significant accuracy differences between any of the conditions.

Eye-position monitoring. An alternative account of the present results holds that the transient shift-related activity we observed in SPL (**Figs. 4** and **5**) might be due to an increase in eye movements after shift targets compared to hold targets, despite our instruction to maintain fixation. Regions within the SPL are thought to contain cells that control eye movements[44].

To evaluate this possibility, five of the participants completed three runs of the experimental task outside the scanner while their eye position was recorded with an EyeLink video-based eye tracking system (SMI, Teltow, Germany). An eye movement was registered if the velocity exceeded 30°/s or if the acceleration exceeded 9,600°/s² for 8 ms within a 1,000-ms temporal window following the appearance of each target (blinks were excluded). Subjects made few eye movements on average (0.56 ± 0.18, 0.39 ± 0.19, 0.53 ± 0.13 and 0.51 ± 0.1 after hL, sR–L, hR and sL–R targets, respectively). A two-way ANOVA revealed no significant differences in the number of eye movements after shift versus after hold events ($F_{(1,4)} = 0.48$, $P > 0.6$). Expanding the inclusion window to 2,000 ms did not change the results.

MRI scanning and data analysis. In Baltimore, data were collected with a Philips Gyroscan scanner (1.5 T, Philips Medical Systems, Best, The Netherlands). Anatomical images were acquired using an MP-RAGE T1-weighted sequence optimized for gray:white matter contrast that yielded images with a 1-mm isovoxel resolution (TR = 8.1 ms, TE = 3.7 ms, FA = 8°, time between inversions = 3 s; inversion time = 748 ms). Whole brain echoplanar functional images (EPI) were acquired with a Philips end-capped quadrature head coil in 15 or 16 transverse slices (TR = 1000 ms, TE = 35 ms, FA = 90°, matrix = 64 × 64, FOV = 240 mm, slice thickness = 7 or 6 mm, no gap).

In Nijmegen, data were acquired with a Siemens Sonata scanner (1.5 T, Siemens Medical Solutions, Erlangen, Germany). Anatomical images were acquired using an MP-RAGE T1-weighted sequence that yielded images with 1 mm isovoxel resolution (TR = 8.8 ms, TE = 3.93 ms, FA = 15°). EPIs were acquired in 20 transverse slices (TR = 1600 ms, TE = 40 ms, FA = 90°, matrix = 64 × 64, FOV = 256 mm, slice thickness = 5 mm, 0.5 mm gap between slices). Before combining the data from Nijmegen and Baltimore, the timeseries data were resampled to millisecond resolution to compensate for the disparate TRs.

Brain Voyager software (Brain Innovation, Maastricht, The Netherlands) was used for the fMRI data analyses. Images were slice-time and motion corrected before high pass temporal frequency filtering removed components that occurred three or fewer times per run. The images were then Talairach-transformed and resampled into 3-mm isotropic voxels. A 4-mm FWHM Gaussian kernel was used to spatially smooth the data before the group analysis was carried out.

An idealized time series was created for each of the four event types by convolving a boxcar function marking the temporal position of each event with a gamma function (**Supplementary Fig. 1** online; ref. 45, δ = 2.5, τ = 1.25). For group analyses, a random effects general linear model (GLM) was used to estimate a beta weight for each regressor; for single-subject analyses, we used a fixed-effects GLM. A correction for serial correlation was used for all analyses. The mean lag-1 autocorrelation for the group GLM was 0.26 before the correction and –0.01 after the correction.

The data from single subjects reported in **Figs. 2** and **4** were corrected for multiple comparisons made within the brain volume (Bonferroni, $P < 0.01$). The single voxel threshold in the group data depicted in **Figs. 3, 5** and **6** was set at $t_{(12)} = 4.0$, $P < 0.002$. The single voxel threshold for the group of eight subjects depicted in **Fig. 7** was set at $t_{(7)} = 4.8$, $P < 0.002$. A minimum cluster size of 0.4 ml was adopted to correct for multiple comparisons, yielding a whole brain corrected statistical threshold of $P < 0.005$ as determined by AlphaSim (B. D. Ward, http://afni.nimh.nih.gov/afni/docpdf/AlphaSim.pdf; 10,000 simulations with a brain volume of 1,638 ml and 4 mm FWHM spatial smoothing).

articles

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