Control of Visuotemporal Attention by Inferior Parietal and Superior Temporal Cortex

Kimron Shapiro,1 Anne P. Hillstrom,2 and Masud Husain3,4,5
1School of Psychology
University of Wales
Bangor LL57 2AS
United Kingdom
2Department of Psychology
University of Texas
Arlington, Texas 76019-0528
3Division of Neuroscience
and Psychological Medicine
Imperial College School of Medicine
Charing Cross Hospital
London W6 8RF
4Institute of Cognitive Neuroscience
UCL
London WC1N 3AR
United Kingdom
5Correspondence: m.husain@ic.ac.uk

Summary
The human cortical visual system is organized into two major pathways: a dorsal stream projecting to the superior parietal lobe (SPL), considered to be critical for visuospatial perception or online control of visually guided movements, and a ventral stream leading to the inferotemporal cortex, mediating object perception [1–3]. Between these structures lies a large region, consisting of the inferior parietal lobe (IPL) and superior temporal gyrus (STG), the function of which is controversial. Lesions here can lead to spatial neglect [4, 5], a condition associated with abnormal visuospatial perception [6, 7] as well as impaired visually guided movements [8, 9], suggesting that the IPL + STG may have largely a “dorsal” role. Here, we use a nonspatial task [10] to examine the deployment of visuotemporal attention in focal lesion patients, with or without spatial neglect. We show that, regardless of the presence of neglect, damage to the IPL + STG leads to a more prolonged deployment of visuotemporal attention compared to lesions of the SPL. Our findings suggest that the human IPL + STG makes an important contribution to nonspatial perception, and this is consistent with a role that is neither strictly “dorsal” nor “ventral” [11]. We propose instead that the IPL + STG has a top-down control role, contributing to the functions of both dorsal and ventral visual systems.

Results and Discussion
The attentional blink paradigm provides a measure of the temporal dynamics of visual processing: the time taken by the visual system to identify a visual stimulus before it is free to detect a subsequent stimulus [10, 12]. When healthy elderly participants identify a target object (T1) in our task (Figure 1), their ability to detect a second visual target (T2) is impaired if it appears within 360 ms of T1 [7]. During this brief period, termed the “attentional blink”, approximately 30% of T2 stimuli go undetected, failing to reach awareness.

In the present study, four non-neglect patients with IPL + STG lesions — three in the left hemisphere and one in the right hemisphere (lesions are shown on one hemisphere in Figure 2A) — were tested. In the attentional blink paradigm, they showed a more severe and prolonged deficit than healthy elderly individuals. Figure 3A shows that less than 50% of T2 stimuli were detected if they were presented 180–720 ms after T1. Thereafter, performance improved dramatically, with 83%–90% of T2 stimuli being detected. Comparison with the baseline single-report condition (where participants identify only T2 and ignore T1) shows a statistically significant attentional blink lasting for 540 ms, with significant differences between the two conditions at 180, 360, and 540 ms (t[3] = 2.37, p < 0.05; t[3] = 5.01, p < 0.01; and t[3] = 3.23, p < 0.05, respectively). Mean T1 identification was 81%, demonstrating that IPL + STG patients were actively attempting to identify T1 in the dual-report task. Furthermore, in the single-report baseline condition when only T2 needs to be detected, accuracy ranged from 81%–91%, showing that the attentional blink observed in the dual-report condition is not due simply to a failure to sustain attention for the duration of a trial.

The SPL patients we tested also did not suffer from spatial neglect. Their greatest lesion overlap lay on the superior convexity and dorsomedial surface of the parietal lobe, all in the right hemisphere (Figure 2B). In our attentional blink paradigm, these patients behaved quite differently than the IPL + STG group. Figure 3B shows that, for SPL patients, only 26% of T2 stimuli were undetected if presented within 360 ms of T1, and this resembled more closely the performance of healthy control individuals than IPL + STG patients. Comparison with the baseline single-report condition shows a statistically significant attentional blink at 360 ms (t[3] = 2.47, p < 0.05). A significant effect was not found at 180 ms, perhaps because of the relatively slow sequences used compared to studies in younger subjects (see the Experimental Procedures) or the small sample size of our group. Mean T1 identification for the SPL group was 91%, demonstrating that, like the IPL patients, they were actively engaged in identifying T1. T2 detection in the baseline single-report condition ranged from 78%–100%, demonstrating that the performance of SPL patients in the dual-report condition also could not be explained by a loss of sustained attention.

Thus, in patients without spatial neglect, damage to the IPL + STG leads to a prolonged and more severe impairment in visuotemporal attention than SPL lesions. However, because all of our SPL patients had right hemisphere lesions and most of our IPL + STG group had left hemisphere damage, it could be argued that any
Figure 1. Attentional Blink Paradigm
An example of a typical sequence, showing only some of the stimuli (all subtending ~1.4° in height and 0.7° in width from a viewing distance of 35 cm). All sequences contained only one white letter (T1 or Target 1), which is an “N” in this case. All other stimuli were black. The number of items before T1 varied between 7 and 15. T2 (Target 2) was always a black “X”. In this example, T2 is shown as the third letter in the nine-letter sequence following T1. Sequences of stimuli were similar in dual- and single-report trials, but participants were asked to make different types of reports. In dual-report trials, at the end of a sequence, they reported the identity of the white letter (T1) as well as reported whether a black “X” (T2) had been present. In single-report trials, at the end of a sequence, they had to report only whether a black “X” (T2) had been present. Responses were unspeeded, with the experimenter typing in the reports made by the patients and starting the next sequence thereafter. Ten sequences were displayed in each block of trials, with subjects being told at the beginning of each block whether it was a dual- or single-report block.

Figure 2. Lesions of the IPL + STG and SPL Groups
(A–C) For the non-neglect IPL + STG patients (mixed left and right hemisphere lesions), the zone of maximum overlap is in the posterior angular gyrus (all lesions drawn on one hemisphere). (B) For the non-neglect SPL group (all lesions in the right hemisphere), the maximum overlap is on the superior convexity and dorsomedial surface of the superior parietal lobe. (C) The maximum overlap of the IPL + STG patients with neglect (all lesions in the right hemisphere) is in the supramarginal gyrus. Light green represents the overlap of three lesions, blue represents the overlap of two lesions, and purple represents one lesion.
comparison is confounded by hemispheric differences. To address this issue directly, we looked at the performance of a group of three right hemisphere IPL+STG patients (Figure 2C). All of these patients had left-sided visual neglect, as determined by performance on standard cancellation and line bisection tests [13, 14]. They were part of a larger group of patients with neglect that we studied previously using the attentional blink paradigm [7], but their data has not previously been presented separately.

These right IPL+STG patients showed a protracted and deep impairment in detecting T2 in the dual-report condition (Figure 3C). Comparison with the baseline single-report condition shows a statistically significant attentional blink at 360, 540, 900, and 1260 ms (t[2] = 3.21, t[2] = 3.82, t[2] = 6.43, t[2] = 3.60, respectively; p < 0.05 for all), with mean single-report performance ranging from 71%–92%. They detected T1 in 74% of the trials. Thus, these right hemisphere IPL+STG patients have an attentional blink that is longer lasting than in the right SPL patients.

Taken together, our findings demonstrate abnormal attentional blink functions following either left or right IPL+STG lesions (although right hemisphere patients with neglect performed worse than their left hemisphere counterparts). By contrast, right SPL patients performed like healthy elderly control subjects. Could the difference between IPL+STG and SPL groups be due simply to the fact that SPL lesions may not affect foveal visual processing, whereas IPL+STG damage might? This seems very unlikely since all patients, regardless of lesion location, performed the single-report control task (which also required foveal processing) well. The differences between the groups emerged in the dual-report condition, which suggests an abnormal deployment of visuotemporal attention in the IPL+STG patients (for further discussion of this rationale, see [10, 12]).

Many previous investigations have demonstrated a role for the human IPL+STG in either spatial perception or action [4, 6, 8] and suggest that this region is part of the dorsal stream. But, consistent with our proposal that this area also has a nonspatial role, activation in part of the IPL+STG complex has been observed by three recent functional imaging studies of visuotemporal attention [15–17]; although, unlike lesion studies, these investigations cannot demonstrate that this area is necessary for nonspatial functions. Taken together with the results of these previous investigations, our findings suggest that the IPL+STG has features of both the (spatial) dorsal and the (nonspatial) ventral stream.

Milner has hypothesized that the IPL+STG might represent a nexus between dorsal and ventral streams, although he has emphasized that inputs from the ventral
system may be particularly critical [11]. The data presented here would be quite compatible with such a proposal. However, we propose an alternative view and suggest instead that the IPL+STG has a role in the top-down control of visual and visuomotor processing. Specifically, we suggest that it biases information flow within both the ventral and dorsal streams.

How could such a model explain the abnormal deployment of visuotemporal attention in IPL+STG patients? Work in healthy individuals suggests that the attentional blink reflects impaired selection of critical items (i.e., targets) competing within the stream of letters [10]. A control mechanism is necessary to resolve such competition. Our data would be consistent with such top-down control being mediated by the IPL+STG. By contrast, recent models of attention have proposed that top-down control is the province of the frontal cortex [18, 19]. However, functional imaging reveals IPL+STG, as well as frontal, involvement [20]. Furthermore, both lesion and imaging studies have implicated the IPL+STG region in redirecting attention from cued locations toward unexpected visual stimuli [21, 22], and this is indicative of a top-down control role. Selection of targets competing for visuomotor control may also be mediated by the IPL+STG. Patients with lesions here demonstrate a bias to direct saccades to ipsilesional stimuli that cannot be attributed to a perceptual deficit [23] but may be accounted for by a top-down spatial bias in visuomotor control.

Regarding the functions of the SPL, our findings do not suggest a role for this region in visuotemporal perception, at least in so far as the task demands required in the present paradigm. In keeping with several other lines of evidence [1, 2], we would consider this region in humans to be analogous to the endpoint of the dorsal pathway in monkeys. Future work will need to establish the exact boundaries between the human dorsal and ventral systems, as well as the area between—the IPL+STG complex—which we propose has both dorsal and ventral functions.

The intraparietal sulcus (IPS), dividing SPL from IPL, is a particularly difficult region to assign. Several neuroimaging studies have implicated parts of the IPS in controlling saccades or grasping movements [24, 25] and suggest a “dorsal” role for this region. However, other investigators have found IPS activation in foveal perceptual tasks that do not require spatial orienting of gaze or attention [15–17, 26–28], and these findings suggest a “ventral” function. Similarly, electrophysiological studies have demonstrated selectivity for shapes presented in foveal vision within a saccade-related region in monkey IPS [29]. Human lesion studies, too, have not been able definitively to distinguish whether IPS is largely dorsal or ventral, since the disorders of reaching and grasping that have been reported in patients with IPS damage also involve the convexity of the SPL [30].

In the present study, the demarcation zone between SPL and the IPL+STG was around the superomedial IPS. We chose this region for two reasons. First, a recent detailed functional imaging study has demonstrated a visuomotor region just medial to the superomedial tip of the IPS [31], so this region is likely to be part of the dorsal system. Second, two of the SPL patients in our study misreached to visual targets (optic ataxia), and this is considered to be a “dorsal impairment” [1]. The area of damage common to both individuals was the superior convexity of the SPL, but one patient’s lesion did encroach on the superomedial IPS, so both of these regions may be part of the human dorsal system. In monkey, the parietal reach region is situated in a homologous location, on the superior convexity and extending to the superomedial IPS [32]. Although it is possible that the anatomical demarcation between SPL and IPL+STG that we have used may need to be revised in the future, we believe that it is a reasonable one, given our current knowledge. Moreover, what remains clear, regardless of precise assignment, is that patients with lesions categorized as IPL+STG in this study have a deficit in deploying visuotemporal attention that is not seen in patients that we classified as having SPL lesions.

Clearly, though, more detailed investigations of the specific contributions of subregions within the human IPL+STG complex are required. Despite the lack of such precise information, we suggest that the human lesion data broadly points to an important distinction between the dorsal stream (to SPL), ventral stream (to the inferior temporal cortex), and the region that lies between them—the IPL+STG complex—that is neither strictly dorsal nor ventral.

Experimental Procedures

Attentional Blink Paradigm

All subjects viewed a stream of letters presented successively at the center of a laptop computer display from a viewing distance of 35 cm. Each letter was presented for 131 ms with an interstimulus interval of 49 ms, yielding a presentation rate of 5.5 letters/s (Figure 1). This is half the rate normally used in studies with young healthy volunteers [12], but we have used this slower rate in a previous study with patients and healthy elderly control subjects [7]. Letters subtended approximately 1.4° of the visual angle in height and 0.7° in width. All letters were black, except for the first target letter (T1), which was white. The background was a uniform gray field that was present throughout the sequence. The experimenter initiated a trial by depressing a computer key. Each trial began with a 360-ms presentation of a small white fixation dot. The number of letters presented before T1 varied randomly between 7 and 15. T1 appeared in all trials and was always followed by a sequence of nine letters (Figure 1). T1 could be any letter in the alphabet, except “X”.

The second target (T2) was a black “X”, appearing in a randomly chosen half of the trials. T2 was never presented prior to T1 and never appeared twice within a single stream.

Participants were instructed in separate trial blocks to report the presence or absence of T2 alone (single-report trials that serve as a baseline control) or to identify T1 as well as report whether T2 was present (dual-response trials). Subjects waited until the stream of letters had been terminated before making their report. Previous reports show that the vast majority of errors in reporting T1 arise from reporting the item either just preceding or succeeding T1 [12, 33]. It is likely, therefore, that a correct report of either $T - 1$ (the item preceding T1) or $T + 1$ (the letter following T1) indicates that participants were attending to T1. In this study, we considered T1 to be correct if the report of the first target was $T - 1$, the actual T1 target, or $T + 1$ item. T2 was presented 10 times at each of the 9 possible serial positions after T1, yielding a total of 90 T2-present trials and 90 T2-absent trials for each condition (single- or dual-response). Subjects received one block of judging T1 alone, eight
blocks of judging both T1 and T2, and eight blocks of judging T2 alone. There were 20 trials in each block. The order of conditions was counter-balanced across subjects to as great an extent as possible. Within a block, T2 was randomly presented once at each of the nine serial positions following T1. The statistical analyses reported were one-tailed Student’s t tests.

Patients

Eight non-neglect patients with focal posterior lesions were tested no sooner than six weeks following stroke. Our previous study with right hemisphere patients demonstrated a relationship between abnormal attentional blink and spatial neglect [7]. In the present study, we first excluded patients with neglect so that we could investigate whether there is a visuotemporal deficit in IPL- STG patients who do not suffer from a spatial deficit. At the time of testing, therefore, none of these eight patients had neglect on the basis of clinical observation or formal testing using cancellation, line bisection, or drawing tests [13, 14]. We also excluded patients with dysphasia. Four individuals had lesions involving the right SPL. Two of them demonstrated optic ataxia and misreached to visual targets [2, 30] at some stage after their stroke. The other four patients had more inferior lesions, all involving the IPL and, in three cases, also extending into the STG. Three of these patients had left hemisphere lesions, and one had right hemisphere damage.

Because all of our SPL patients had right hemisphere lesions and most of our IPL- STG patients had left-sided damage, we also looked at the performance of three right IPL- STG patients, all with left-sided neglect. These patients came from a larger cohort of neglect patients that we have studied previously [7]. They allowed us to compare the performance of our right SPL patients with a group of right IPL- STG individuals.

Lesions were plotted onto a standard template brain by using MRIcro software [34]. Figure 2A shows that the SPL group had the greatest lesion overlap on the superior convexity and dorsomedial surface of the parietal lobe. One patient’s lesion abutted the medial bank of the intraparietal sulcus; the other three patients’ lesions did not involve the intraparietal sulcus. The non-neglect IPL- STG group had the greatest lesion overlap in the region of the posterior angular gyrus (Figure 2B). Three of the patients had damage involving the intraparietal sulcus (IPS), including the lateral bank and fundus. Lesions of the neglect IPL- STG patients are shown in Figure 2C. All three patients had lesions involving the lateral IPS; two patients’ lesions extended into the STG.

Acknowledgments

We thank the patients who kindly participated in this study. This work was supported by grants from The Wellcome Trust to K.S. and M.H.

Received: April 16, 2002
Revised: May 16, 2002
Accepted: June 13, 2002
Published: August 6, 2002

References