Converging levels of analysis in the cognitive neuroscience of visual attention

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Experiments using behavioural, lesion, functional imaging and single neuron methods are considered in the context of a neuropsychological model of visual attention. According to this model, inputs compete for representation in multiple visually responsive brain systems, sensory and motor, cortical and subcortical. Competition is biased by advance priming of neurons responsive to current behavioural targets. Across systems competition is integrated such that the same, selected object tends to become dominant throughout. The behavioural studies reviewed concern divided attention within and between modalities. They implicate within-modality competition as one main restriction on concurrent stimulus identification. In contrast to the conventional association of lateral attentional focus with parietal lobe function, the lesion studies show attentional bias to be a widespread consequence of unilateral cortical damage. Although the clinical syndrome of unilateral neglect may indeed be associated with parietal lesions, this probably reflects an assortment of further deficits accompanying a simple attentional imbalance. The functional imaging studies show joint involvement of lateral prefrontal and occipital cortex in lateral attentional focus and competition. The single unit studies suggest how competition in several regions of extrastriate cortex is biased by advance priming of neurons responsive to current behavioural targets. Together, the concepts of competition, priming and integration allow a unified theoretical approach to findings from behavioural to single neuron levels.

Keywords: visual attention; neglect; functional imaging; visual cortex

1. INTRODUCTION

In any normal visual environment, filled with a complex clutter of overlapping objects and surfaces, three aspects of the attentional problem are immediately evident. First is limited attentional capacity: at any given moment, only a small fraction of the total visual input is actively taken up and used in the control of behaviour. In this sense objects compete to be processed. Second is top-down control or selectivity based on relevance to behaviour: given attentional competition, it is important to deal selectively with those particular objects of relevance to current concerns. Third is integration (Treisman, this issue; Treisman & Gelade 1980): generally speaking, behaviour directed to some chosen object—e.g. reaching to pick up a specified object from a table—will require that several separate properties of that object (shape, location, orientation and so on) be selected and processed together.

Much is now known of the many regions of the primate brain that are concurrently activated by visual input. In the posterior cerebral cortex these include several 'visual areas', specialized for different purposes and in part for the processing of different visual attributes such as shape, motion, and spatial position (Zeki 1978; Desimone & Underleider 1989). In anterior cortex, visually driven activity is also seen in several more 'motor' areas, including frontal eye fields, premotor cortex and so on. Also included should be subcortical structures, including the superior colliculus and several nuclei of the thalamus. In this paper, the problems of competition, integration and top-down control are considered in light of this widely distributed brain activity.

One conventional view is that selective visual attention is the province of spatial processing structures, in particular the parietal lobe (see, for example, De Renzi 1982). According to a simple version of this view, each parietal lobe is predominantly responsible for directing attention to the contralateral side of stimulus space, though a number of more sophisticated versions have also been proposed (see, for example, Mesulam 1981; Posner *et al.* 1984). In this paper I present a somewhat different view, the integrated competition hypothesis (Desimone & Duncan 1995; Duncan 1996; Duncan *et al.* 1997*a*), and experiments bearing on it from levels of normal and impaired human behaviour to functional neuroimaging and single unit electrophysiology.

2. INTEGRATED COMPETITION HYPOTHESIS

The integrated competition hypothesis rests on three general principles.

1. As already detailed, several brain systems are concurrently activated by visual input. Our hypothesis suggests that, in many and perhaps most of these systems, processing is competitive: enhanced response to one object is associated with decreased response to others. For example, responses to different objects may be mutually inhibitory.

At the behavioural level, we take competition to be reflected in the interference that generally occurs when a person must divide attention between different objects in a visual scene. Many previous experiments have detailed properties of this interference, which occurs whether objects are presented at widely separate locations or overlapping at the point of fixation (Duncan 1984; Vecera & Farah 1994), and whether the person is asked to identify similar aspects of the two attended objects, e.g. their shapes or locations, or dissimilar aspects, e.g. the shape of one object and the location of another (Duncan 1993*a*,*b*; for a partial exception, see Duncan & Nimmo-Smith (1996)).

2. Top-down priming of neural activity biases competition towards objects of relevance to current behaviour (Walley & Weiden 1973; Harter & Aine 1984). A good example is the partial report experiment, in which an array of letters (or other objects) is displayed, usually so briefly as to prohibit eye movements. Subjects are asked to identify some of these letters while disregarding others. Consider a subject who is asked to read only the red letters. We propose that, in extrastriate systems coding colour, neurons selective for red inputs are preactivated or primed by this instruction. A largely equivalent possibility is that neurons selective for other colours are deactivated or inhibited. Red letters in the display thus activate primed neurons, and are at a competitive advantage.

   Physiological evidence for such priming will be considered in a later section (see also Desimone, this issue). For the present, the key point is that selective priming gives top-down attentional control its required flexibility. In different behavioural contexts, inputs of any kind might in principle be the most relevant. Returning to the partial report experiment, the instructed selection rule can be based on location (e.g. report only letters from a specified row; see Sperling 1960), on assorted object properties (e.g. report only letters of a specified colour, size, or direction of motion; see von Wright 1968), or even on more complex categorizations (e.g. report letters while ignoring digits; Merikle 1980; Duncan 1983). In all these cases, there is evidence for preferential target processing; in particular, performance depends more on the number of targets than the number of nontargets in a display (Duncan 1980; Bundesen *et al.* 1985; Shibuya 1993). Thus, many different visual properties can be used to direct attention or assign limited processing capacity to objects of relevance to current behaviour. According to our hypothesis, such control is implemented by differential patterns of neural priming, very likely in different extrastriate regions coding the multiple properties of visual input.
3. Competition, finally, is integrated between components of the sensorimotor network (see, for example, Farah 1990; Mesulam 1990). As an object gains dominance in any one system, responses to this same object are supported elsewhere. Various network models have been proposed to account for how such integration might occur (see, for example, Phaf *et al.* 1990). For present purposes, the key point is that the network as a whole tends to cascade into a state in which the same object is dominant throughout. In this way its numerous properties are made concurrently available for control of different aspects of behaviour.

   Such integration is a functional requirement if whole object selection is to be achieved starting from task-specific, local patterns of neural priming. Returning to partial report, very different priming patterns will doubtless be established by instructions to read red letters, or small letters, or letters in a particular row; in each case, however, the final result must be selective processing of the desired shapes and their names. Integration is also reflected in a robust behavioural result: for many pairs of dimensions, two simultaneous discriminations concerning the same object can be made without loss of accuracy (Duncan 1984, 1993*a*,*b*; Duncan & Nimmo-Smith 1996; see also Lappin 1967; Kahneman & Henik 1977; Treisman *et al.* 1983). While distinct objects compete to be processed, different properties of the same object become available together for report and control of behaviour.

According to the integrated competition hypothesis, attentional functions such as competition and priming are not the specific province of some particular part of the sensorimotor network, such as the parietal lobe. Rather they reflect distributed states of the network as whole. The remainder of this paper presents four lines of experimental work done in the context of this general view. A first set of experiments addresses the domain of attentional competition at the behavioural level. It suggests a substantial modality-specific element to limited processing capacity. A second set of experiments shows lateral attentional imbalance to be a rather common consequence of unilateral brain lesions, irrespective of parietal involvement. Such imbalance may be only one component of the clinical picture of 'unilateral neglect' associated with parietal lesions. A third set of experiments uses functional imaging to implicate joint, competitive activity of occipital and prefrontal cortex in lateral attentional focus. The final experiments detail attentional competition in single neurons of the extrastriate cortex of the macaque, and consider the role of such neurons in top-down attentional control.

3. BEHAVIOURAL STUDIES

A key aspect of the integrated competition hypothesis is competition between concurrent visual representations. In large part, we take such competition to occur in the several extrastriate regions coding different properties of the visual input. A natural prediction might be that competition will be very much weaker when inputs occur in different sensory modalities, and thus are represented in very different sensory systems. Data in support of this prediction were obtained in an early study by Treisman & Davies (1973). Recently, we have extended their methods to provide detailed measurements of attentional competition time-locked to the presentation of critical target stimuli within and between modalities (Duncan *et al.* 1997*b*).

A first experiment used auditory stimuli. In each trial, the subject heard two brief speech streams, spoken concurrently over headphones by two different voices, one high and one low. The impression was of two centrally located voices speaking rapidly and simultaneously for a period of a few seconds. Each stream consisted of a series of non-targets—the syllable 'guh' repeated at a rate of 4 s^{-1}—with a single target word embedded somewhere within it. In any given trial, the first target occurred unpredictably in either the high- or the low-voice stream; the second occurred in the other stream following an interval (stimulus onset asynchrony or SOA) of between 125 and 1375 ms. The task was simply to identify targets, ignoring non-targets. In focused attention conditions, subjects listened only to one voice, high or low for a whole block of trials, and thus identified only one word per trial. In divided attention conditions, subjects listened to both voices and identified both targets in each trial. In all cases, the indication of which target or targets had been heard was made after the whole stimulus sequence had finished.

Results are shown in figure 1*a*. In this figure, the accuracy of identifying the first target in any given trial is shown at negative SOA, while second target data appear at positive SOA. Data at −125 ms, for example, show performance for a first target presented 125 ms before a second. Comparison of focused and divided attention shows two results. First, there was an overall loss of accuracy in the divided attention case. Several factors may contribute to a general difficulty in preparing and executing two concurrent tasks (Pashler 1994); these are not our main concern here. Of more interest is the second finding in the divided attention condition: when one target was followed within a few hundred milliseconds by another, the accuracy of identifying both (in particular the second) was decreased. Interference between targets presented close together in time is a common result in experiments of this sort (Broadbent & Broadbent 1987; Raymond *et al.* 1992; Duncan *et al.* 1994; see also Ostry *et al.* 1976; Duncan 1980). A time-course of a few hundred milliseconds is typical of such interference. Subjectively, attention is committed to the first target and is then unavailable for the second.

The visual case was examined in a second experiment. With one complication, events and timing were copied closely from the auditory study. The complication concerns event streams, which were designed so that, even in focused attention conditions, it would always be optimal to keep the eyes fixated on the centre of the display. Each event in the 'horizontal stream' was a pair of letter strings, flashed briefly and simultaneously to the left and right of fixation. For non-targets, both letter strings were rows of three 'x's. For targets, one string (at random either left or right) was a three-letter word to be identified. As before, events (flashes) followed one another in rapid succession, at a rate of 4 s^{-1}. The 'vertical stream' was similar, except that the components of each flash appeared one above and one below fixation. As for high and low voices in the auditory study, horizontal and vertical streams were presented concurrently for a period of a few seconds. Overall, therefore, the subject saw rows of 'x's flashing rapidly and concurrently in all four screen locations, with one target presented at some time during the trial to left or right of the fixation point, and another above or below. Again, the divided attention case (identify both targets) was compared with focused attention controls (identify only the horizontal target in some trial blocks, only the vertical target in others). Results, shown in figure 1*b*, were very much as before. In the divided attention condition, again, there was substantial interference when successive targets occurred within an interval of a few hundred milliseconds.

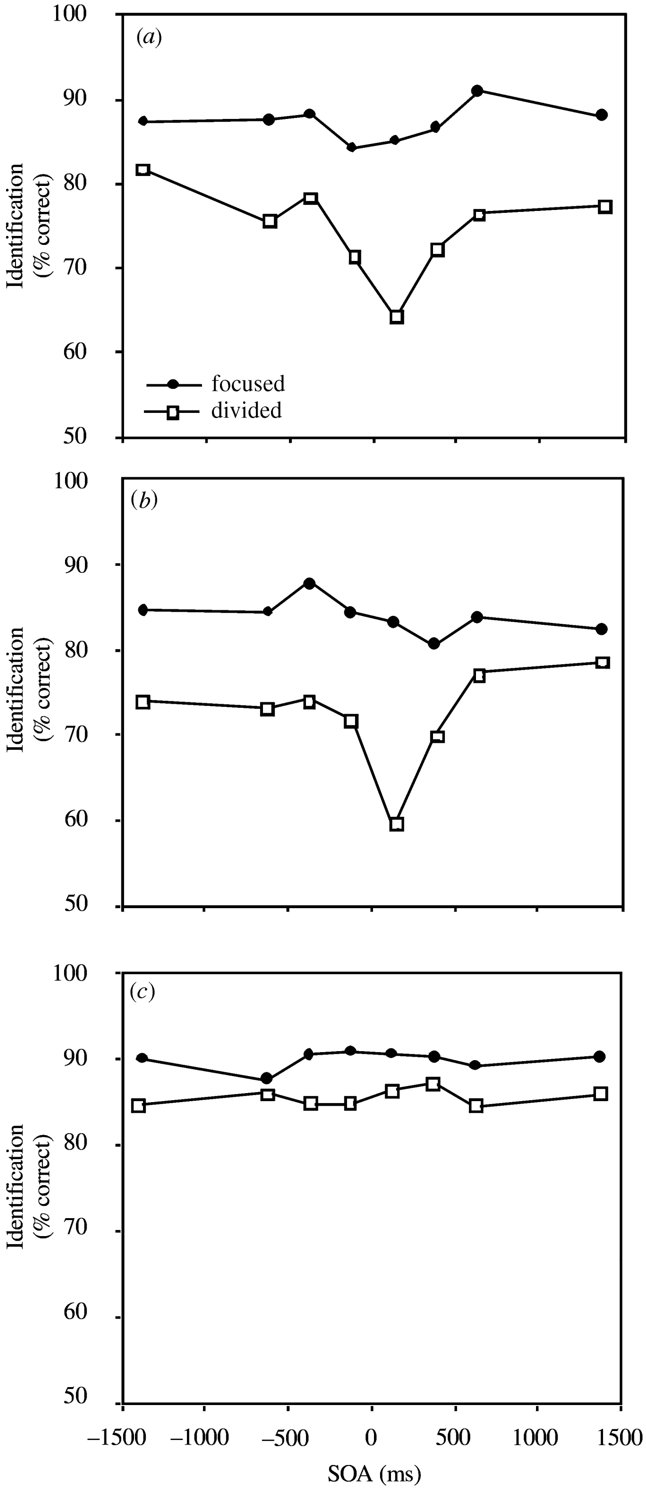

Figure 1. Focused and divided attention performance within and between modalities: (*a*) auditory; (*b*) visual; (*c*) mixed modality. Score is per cent correct target identification as a function of between-target interval. Adapted with permission from Duncan *et al.* (1997*b*).

The results of auditory and visual studies are remarkably similar. Does this indicate some common, general limit on the capacity to process concurrent stimulus events? The answer is provided in the third experiment, in which concurrent targets came from separate sensory modalities. For this experiment, the high voice stream of the auditory experiment was combined with the horizontal stream of the visual experiment. Again each stream contained a single target, with details of timing and procedure exactly as before. Results are shown in figure 1*c*. Again there was a general loss of accuracy associated with the requirement to perform two tasks at once. This time, however, there was absolutely no interference time-locked to target presentation. Under the circumstances of this experiment, directing attention to a target in one modality left concurrent processing in a different modality undisturbed.

In our experiments, all stimuli were located close to the central or straight-ahead position. Auditory stimuli were presented binaurally over headphones, while visual stimuli were all presented within about 2° of central fixation. A somewhat separate issue arises in experiments with large angular separations between inputs in different modalities. As one example, Driver & Spence (1994) presented concurrent auditory and visual stimuli from speakers–screens positioned approximately 30° to left and right of body midline. Under these circumstances, concurrent identification of the two inputs was much better when they originated on the same side. The results are strongly reminiscent of our proposal that the same selected input tends to become dominant throughout the sensorimotor network. When inputs arise from widely separate locations, there is a clear preference for auditory and visual systems to converge to work on the same general area of space (Kinsbourne 1987). Similar results in other studies suggest spatial integration of visual, auditory, postural, tactile, and even motor systems (see Driver, this issue; Morais 1978; Robertson & North 1994; Driver & Grossenbacher 1996). When all inputs are close to central, however, our results show substantial independence in the processing of visual and auditory targets. Under these circumstances, the results imply that the principal basis for attentional competition lies in modality-specific sensory systems.

4. LESION STUDIES

Lesion studies provide a principal motivation for the conventional association of visual attention with the parietal lobe. In the human, parietal lesions (in particular on the right) are often associated with a clinical picture of hemispatial or contralateral neglect. Such neglect is manifest in a general tendency to disregard the side of space opposite to the lesion. Examples include failure to complete the left half of drawings, or to mark left-sided targets when asked to cross out lines in a jumbled spatial array (Bisiach & Vallar 1988).

For several reasons, neglect has often been considered to reflect attentional bias. Particularly relevant is an element of the disorder termed extinction: in some cases, contralesional inputs are only disregarded in the presence of simultaneous, competing inputs on the unaffected or ipsilesional side (Bender 1952; Karnath 1988). Such results strongly imply lateral bias in the normal process of attentional competition.

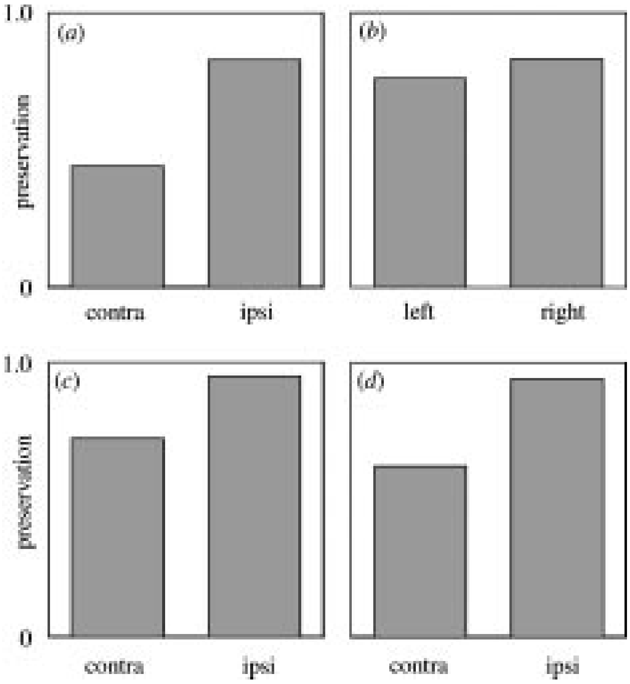

Figure 2. Divided attention performance for three patient groups and matched controls: (*a*) right parietal; (*b*) control; (*c*) right other; (*d*) left occipitotemporal. Preservation score (proportion correct in divided attention divided by proportion correct in single target controls) is shown separately for contralesional (contra) and ipsilesional (ipsi) visual fields. For controls the corresponding separation is simply left compared with right field.

A recent study, done in collaboration with the groups of Claus Bundesen in Copenhagen and Glyn Humphreys in Birmingham, suggests a different perspective (Duncan *et al.* 1998). In combination with others, our findings suggest that extinction or lateral bias may be a very widespread consequence of unilateral brain injury. The gross clinical disorder associated with right parietal lesions arises through combination of this general lateral bias with one or more further impairments, in some cases influencing both sides of space. In our experiments, several methods are combined to measure distinct components of attentional impairment. Here, I shall give just a brief description of two aspects of the results.

To measure extinction or lateral bias we use a standard divided attention method. In single target control trials, the patient is asked to identify letters flashed singly to left or right of fixation. In divided attention trials, letters are flashed simultaneously to left and right, and the patient must identify both. Displays are too brief to permit eye movement, and central fixation is monitored at the start of each trial. For individual patients, exposure duration is adjusted to bring accuracy into a suitable range to avoid ceiling and floor effects.

Results for several subject groups appear in figure 2. For letters in each visual field we calculate a preservation score reflecting how well accuracy is maintained in divided attention. This score is simply proportion correct in divided attention trials divided by proportion correct in single target controls. A score of zero in the contralesional

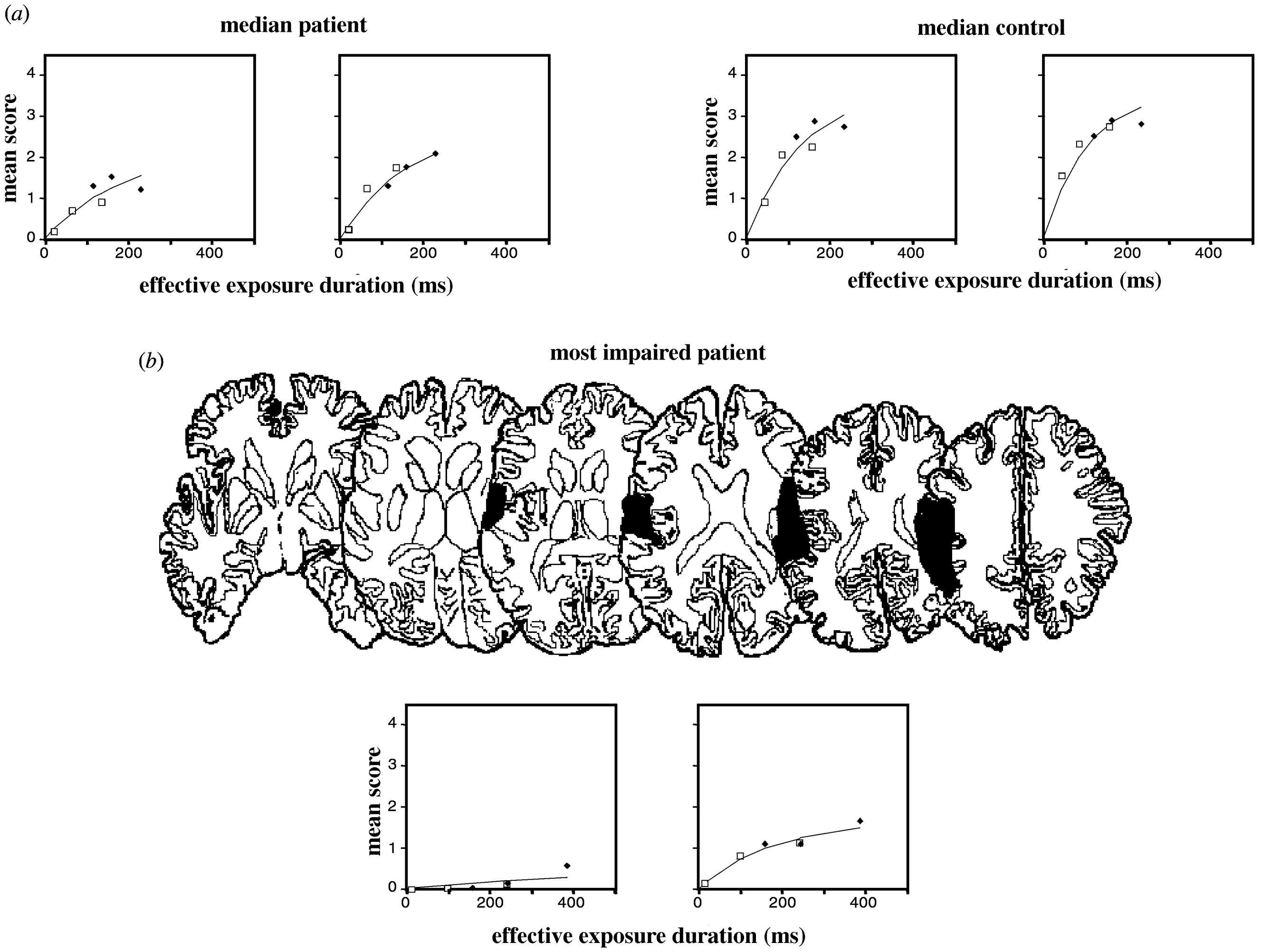

Figure 3. (*a*) Whole report data for median parietal patient and median control. Scores for each subject are mean numbers of letters correctly reported as a function of effective exposure duration, separately for left-field (left panel) and right-field (right panel) arrays. Calculation of effective exposure depends on a curve-fitting procedure described in Duncan *et al.* (1998), applied to data from masked (open squares) and unmasked (filled diamonds) displays. Solid curve is a fit to the data based on whole report theory of Bundesen (1990). (*b*) Patient with most severe impairment. The upper diagram shows the restricted inferior parietal lesion, drawn on standard slices from Gado *et al.* (1979). These slices show the right hemisphere on the left. Whole report data appear below. Adapted with permission from Duncan *et al.* (1998).

field, for example, would indicate complete extinction by an accompanying ipsilesional target.

In figure 2*a* are shown mean results for a group of six patients with lesions of the right parietal lobe, in some cases extending into adjacent areas. The results show a typical extinction pattern; while letters on both sides suffer in divided attention (preservation score less than 1.0), this cost is carried predominantly by the contralesional (left-sided) items. Controls (seven subjects, figure 2*b*) show no such result; though mean data suggest a slight tendency for poorer preservation on the left, this was weak and inconsistent across individuals. These are exactly the results that would be predicted by the conventional parietal lobe hypothesis.

One reason for doubting this hypothesis comes from small groups of patients with other posterior lesions. In figure 2*c*, it shows mean results for two patients with right posterior lesions not involving the parietal lobe. Figure 2*d* shows results for a single patient with an occipitotemporal lesion in the left rather than the right hemisphere (Duncan 1996). In both cases there is the standard extinction result, with preservation scores close to 1.0 for the ipsilesional field, but substantially lower for the contralesional field.

In fact, our results are in line with several other studies showing that extinction can arise after many different kinds of cortical and subcortical lesions (for examples, see Bender 1952; Desimone *et al.* 1990; Vallar *et al.* 1994). These are very much the results to be expected according to the integrated competition hypothesis. Once a part of the sensory input becomes dominant in any region of the sensorimotor network, it will tend to capture control of that network as a whole. Given that many different unilateral lesions may weaken the local representation of contralateral space, the common result should be a generalized competitive disadvantage for that side.

If lateral bias alone is not sufficient to explain the effects of right parietal lesions, what additional factors are involved? Our second set of data concerns total capacity or rate of processing visual input. For this measurement, arrays of five letters were flashed for varying durations in left or right visual field. Subjects simply reported as many as possible. To eliminate lateral bias within an array, letters were presented in a vertical column centred approximately 2.5° to left or right of fixation.

Example results are shown in figure 3. In *a* are shown data from the median patient in our right parietal group (left), compared with the median control subject (right). For each subject, separate panels show data from left- and right-field arrays. In each case, the number of letters reported increased roughly exponentially with increase in exposure duration. This increase, however, was substantially slower in the patient. The results are representative of the overall comparison between patients and controls; data from the worst patient are shown in *b*, along with a diagram showing this patient's restricted inferior parietal lesion. Importantly, the deficit in processing rate was typically bilateral in these right parietal patients. Although rate was somewhat lower in the left field (see examples in figure 3), the main result was decreased rate in both fields, implying a substantial non-lateralized component to the overall visual impairment (see Robertson 1989; Halligan & Marshall 1994; Husain *et al.* 1997).

Undoubtedly there is much more to be done to clarify the interpretation of these results. Figure 2 might suggest a stronger extinction tendency in parietal than in non-parietal patients, and this should be checked with larger patient groups. We have also observed deficits in overall processing rate in patients with lesions outside the parietal lobe. Additional, more specific deficits may be equally important in understanding the effects of parietal lesions, including perceptual minimization (Milner & Harvey 1995) or even active rejection (Mijovic-Prelec *et al.* 1994) of the neglected field. Already, however, it seems clear that the left sided difficulties of right parietal patients reflect a combination of deficits, including a general lateral bias, common to many unilateral brain injuries, and a gross overall reduction in the rate of visual processing.

5. FUNCTIONAL IMAGING

Control of the lateral focus of attention is also a basic question in our recent functional imaging studies. In these studies we have used positron emission tomography (PET) to measure regional cerebral bloodflow (rCBF) in normal subjects focusing attention to the left or right visual field.

In initial studies (Vandenberghe *et al.* 1997*b*), subjects were shown arrays consisting of two circular grating patches, one to each side of fixation. Each patch varied in two attributes, the orientation of the grating, and the precise location of the patch with respect to a surrounding frame. For each patch, both orientation and location varied randomly and independently from one trial to the next. Potentially, therefore, subjects could be asked to make discriminations of either orientation or spatial location in either left or right visual field, or any combination of these. A fixed task (e.g. orientation discrimination on the left) was performed throughout the period of each 40 s scan. Within this period, trials followed one another at a rate of approximately 36 s^{-1}. For each trial, the display was flashed for 495 ms, and the subject reported the relevant judgement (e.g. left orientation) aloud. Central fixation was required throughout, and monitored by electrooculogram.

The first important results concern focused attention conditions. For these, the subject made only a single discrimination, either orientation or location on either left or right patch. For present purposes, the key contrast is between leftward and rightward attention, orientation and location tasks in fact giving rather similar results.

Results are shown in figure 4. The figure shows regions of significant difference between leftward and rightward attention, based on mean data from orientation and location tasks. In each row, the brain is represented in five horizontal sections running from bottom (leftmost slice) to top (rightmost slice). The upper row shows regions of increased rCBF in leftward as compared to rightward attention; the lower row shows the reverse.

There are three results that are noteworthy. First, leftward attention was associated with increased bloodflow in the occipital cortex of the right hemisphere (upper row, first slice). In agreement with previous studies using both PET (Heinze *et al.* 1994) and event-related potentials (Van Voorhis & Hillyard 1977), such results suggest enhancement of visual processing on the side contralateral to attention. Given predominantly crossed representation in many early visual areas, this is very much the anticipated result. Although in our case the effect was restricted to the right hemisphere, subsequently we have observed symmetrical effects (Vandenberghe *et al.* 1997*a*), in agreement with others' results (for example, see Heinze *et al.* 1994).

Second, and somewhat striking, parietal lobe activity was entirely indifferent to the direction of attention. Instead, we observed substantial activation of the superior parietal lobule in all conditions, compared with a control task requiring no peripheral discriminations. As it was indifferent to the direction of attention, such activation is invisible in figure 4. In all conditions, parietal activation was stronger in the right hemisphere. Similar parietal activation has previously been reported in studies of peripheral attention (see, for example, Corbetta *et al.* 1993; Vandenberghe *et al.* 1996; Nobre *et al.* 1997). Although these studies have sometimes suggested stronger activity on the side contralateral to the attended focus, this has been at best a mild modulation occurring on a baseline of generally stronger activity on the right, and is certainly not visible in our results.

The third result is perhaps the most surprising. Attention to either side was associated with increased activity in the ipsilateral frontal lobe. Thus, leftward attention was associated with a broad band of activation of the left lateral frontal cortex (figure 4*a*, first and third to fifth slices). Rightward attention was associated with a more restricted activation of right lateral frontal cortex (figure 4*b*, third slice). The results suggest an intriguing hypothesis: on each side, one function of lateral frontal cortex may be to inhibit or accord a competitive disadvantage to the contralateral side of space. Indeed, frontal lesions are sometimes associated with disinhibition of unwanted activity on the opposite side, including reflexive eye movements (Butter *et al.* 1988; Paus *et al.* 1991). Neglect of the side ipsilateral to the lesion has also been reported (Kwon & Heilman 1991). Of course, frontal lesions can also be associated with contralateral neglect (Heilman & Valenstein 1972). In some cases, contralateral neglect may reverse as recovery progresses, producing a long-term ipsilateral deficit (Butter *et al.* 1988; Kwon & Heilman 1991).

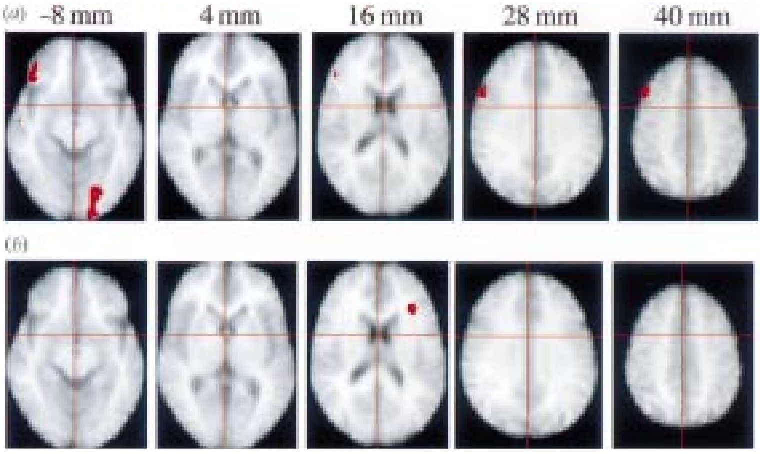

Figure 4. Significant bloodflow differences ($p < 0.05$, corrected for multiple comparisons) between leftward and rightward attention. (*a*) Greater flow in leftward attention; (*b*) the reverse. Each series shows horizontal brain slices progressing from bottom (left) to top (right) of the brain, after averaging between subjects and normalization to the standard space of Talairach & Tournoux (1988). Standard z-levels of each slice are shown at the top of the figure; within each slice, the left of the brain appears on the left. Significant differences are shown in red on the mean of the 14 subjects' normalized magnetic resonance images (MRIs). Analyses conducted using standard SPM software (Friston *et al.* 1995). Adapted with permission from Vandenberghe *et al.* (1997*b*).

Whatever its interpretation, we have found ipsilateral frontal activation to be a consistent result across three separate experiments, involving a variety of tasks and response modes. Illustrative results from our most recent study (Vandenberghe *et al.* 1997*a*) are shown in figure 5. Here the data from one individual subject have been plotted on that subject's own magnetic resonance image to show in more detail the areas of left frontal activity associated with leftward attention. This subject's data illustrate three apparently separate activation foci, each of which is also seen in a number of other subjects. Two are on the lateral surface, one more dorsal, on the middle frontal gyrus, the other more ventral, on the inferior frontal gyrus. The third is buried within the depths of the inferior frontal sulcus. Although these are very preliminary results, they suggest the precision with which single-subject functional imaging may define regions of frontal involvement in controlling (or otherwise reflecting) the attentional focus.

A final set of results concerns divided attention. As we have seen, accuracy suffers when a person must identify properties of two different objects in a single, brief display. Properties of the same object, in contrast, can be identified together without accuracy loss. In a further experiment in our series (Vandenberghe *et al.* 1997*b*), two discriminations were required for each display. In single-object tasks, subjects identified either orientation and location of the left patch, or orientation and location of the right patch. In dual-object tasks, subjects identified either orientation of the left patch and location of the right patch, or vice versa. The results suggest an interesting parallel to two-object performance cost. In both frontal and occipital lobes, extreme patterns of bloodflow were associated with exclusively leftward or rightward attention, while results were intermediate for the two-object case. In left lateral frontal and right occipital cortex, bloodflow was highest for attention to two properties of the left object, lowest for attention to two properties of the right object, and intermediate for attention to one property of each. A complementary pattern was seen in right frontal (although again not left occipital) cortex. The results seem directly to reflect competition between attentional foci, divided attention producing a compromise between the extreme states of cerebral activity associated with focused attention to either one side or the other (Van Voorhis & Hillyard 1977).

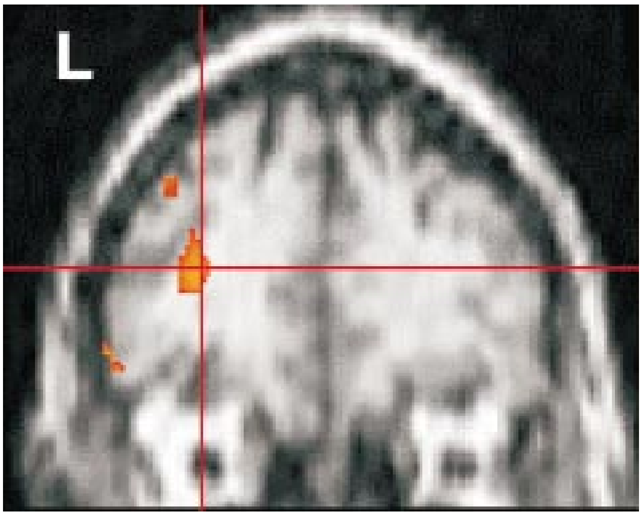

Figure 5. Bloodflow differences ($p < 0.001$, uncorrected) between leftward and rightward attention for a single subject from the study of Vandenberghe *et al.* (1997*a*). Differences (orange–yellow) shown on coronal slice from subject's individual MRI, normalized to standard space of Talairach & Tournoux (1988) and taken at $y = 42$ mm to show prefrontal cortex. Crosshair marks maximum activation in inferior frontal sulcus. Other details as in figure 4.

It is perhaps too soon to draw firm general conclusions from these functional imaging studies. Again, however, the results suggest that lateralized parietal activity may be at best a modest factor in directing attention to the contralateral field. A further consideration may be lateral frontal activity according a competitive disadvantage to contralateral space.

6. SINGLE UNIT STUDIES

The final studies to be considered measure attentional modulation of activity in single cells of the monkey brain. Only an outline of this work will be presented here; for more details see Desimone (this issue).

An illustrative study recorded the activity of single neurons in inferior temporal (IT) cortex during a simple version of visual search (Chelazzi *et al.* 1993, 1998). IT cortex is a high-level visual area whose neurons show selectivity for complex objects and their properties, e.g. complex combinations of colour and shape (Desimone &

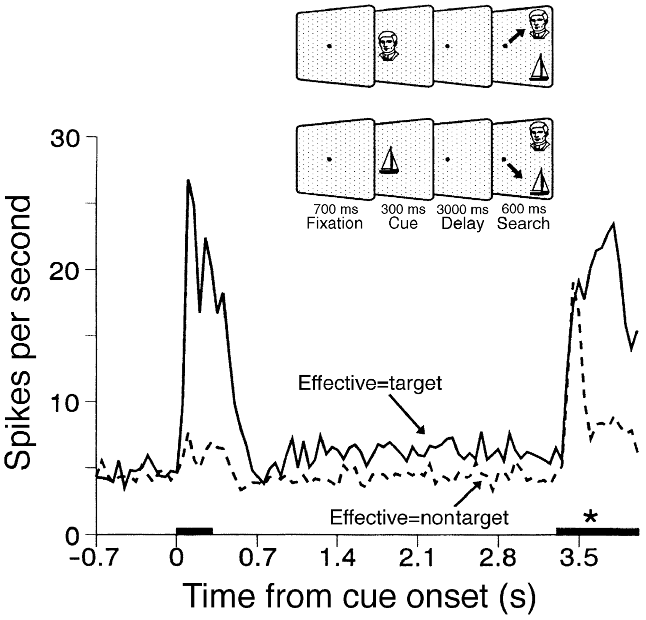

Figure 6. Task and illustrative results from Chelazzi *et al.* (1993). Typical trial events are illustrated at upper right. Effective and ineffective stimuli (see text) are shown schematically as head and boat. Arrow on search display shows required saccade; no arrow was actually presented. Below is shown mean discharge rate (spikes per second) for 22 selective neurons as a function of time from cue onset. On the time axis, first bar marks cue presentation, second bar marks search array, asterisk marks mean time of saccade. Solid line: effective stimulus is cued and becomes target in search array. Dashed line: effective stimulus is uncued and becomes nontarget. Adapted with permission from Desimone & Duncan (1994).

Ungerleider 1989). We asked how such neurons respond when an animal is instructed to select a specific target stimulus from a visual array.

For each neuron isolated, the experiment began by pretesting with a selection of alternative stimuli. Given the complex preferences of IT units, the stimuli we used were digitized magazine pictures. Our aim was to identify two stimuli for use in the main experiment—one, the effective stimulus, producing a strong response from the cell, and a second, the ineffective stimulus, producing little or no response.

Once these stimuli had been identified, the cell's responses were recorded during several hundred trials of the main search task. Each trial began with a central dot on the screen, which the animal was required to fixate (see figure 6, top). Once fixation (measured by scleral search coil) was acquired, a 300 ms cue stimulus was presented, again at screen centre. On different trials this cue was either the effective or the ineffective stimulus. The cue was followed by a delay, during which the animal was simply to maintain central fixation. At the end of this delay, a search array was presented, containing both effective and ineffective stimuli in unpredictable locations within the visual field contralateral to the recording site. The task was to make an immediate saccade from the central fixation point to whichever search stimulus matched the preceding cue.

Mean responses in a population of 22 selective cells are shown at the bottom of figure 6. There are two trial types that can be distinguished, those in which the effective stimulus was cued, and so was the relevant or target stimulus for this trial (solid lines), and those in which it was uncued, and so was an irrelevant non-target (dashed lines). The distinction between effective and ineffective stimuli is shown in responses to the cue (first black bar on time axis). As intended, the effective stimulus produced a substantial response when presented as a cue, while the ineffective stimulus did not. Note, however, that once cues had been removed, subsequent visual input was exactly the same for the two types of trial. Any subsequent difference in neural activity was driven not by current visual input, but by behavioural context.

The first important result concerns activity in the delay interval, when only the fixation point was present on the screen. During this interval, cells fired more strongly when their effective stimulus was the relevant or target stimulus on this trial. Considering IT as a whole, one can conclude that, when a certain stimulus is defined as relevant to a current task, the population of cells responsive to that target shows enhanced or primed activity.

The second important result concerns responses to the search array (second black bar on time axis). Recall that this array always contained the cell's effective stimulus, and so was in principle capable of driving a positive response. Indeed, an initial positive response was always seen, whether or not the effective stimulus was the target. Beginning around 100 ms before the animal's saccade, however, responses on the two types of trial diverged. If the effective stimulus was the target, the response it produced was sustained into the period of the saccade. If the effective stimulus was a non-target, in contrast, the response it produced was rapidly suppressed. Considering IT as a whole, one can conclude that, by the time of the saccade, neural activity is dominated by responses to the relevant or target stimulus.

These results provide a direct motivation for our proposals concerning biased competition in extrastriate cortex. Competition between responses to target and non-target objects is biased by advance priming of the target neural population. The result is sustained response to targets, but suppressed response to non-targets.

The findings concerning selective delay activity have been amplified in a number of further studies. In the above task, behavioural relevance was defined by object identity: the animal was instructed to attend to a particular target object. Correspondingly, we observed selective delay activity in IT cortex, a region specialized for high-level object processing (see similarly Fuster *et al.* 1985; Miyashita & Chang 1988). In other tasks, the instruction is spatial: the animal must attend to whatever object is presented in a specified location. Corresponding spatial delay activity might be unexpected in IT, where receptive fields are large and spatial information correspondingly poor. Instead, it has been reported earlier in the visual system (regions V2, V4); here, cells show enhanced discharge when an animal is instructed to attend to a location lying within the receptive field (Luck *et al.* 1997). Somewhat analogous spatially selective delay activity has also been reported in other areas, including the parietal lobe (Gnadt & Andersen 1988). The results directly support our proposal that different forms of attentional cueing will be implemented by flexible, task-specific forms of neural priming in different extrastriate regions.

In both non-spatial (Fuster *et al*. 1985; Miller *et al*. 1996) and spatial (Niki & Watanabe 1976; Funahashi *et al*. 1989; di Pellegrino & Wise 1993) tasks, particularly strong and robust delay activity is observed in prefrontal cortex. Such results suggest a possible role for the frontal lobe in establishing and preserving top-down attentional bias (Desimone, this issue). Possible mechanisms would include priming of extrastriate cells responsive to current behavioural targets, and (consistent with our functional imaging findings) inhibition of cells responsive to non-targets. Such a role would be in line with the broad importance of the frontal lobe in both working memory function (Goldman-Rakic 1988) and behavioural control more generally (Luria 1966).

The findings concerning non-target suppression have also been amplified in other studies. Stronger responses to relevant than to irrelevant stimuli have been reported throughout much of extrastriate cortex, including areas V2, V4, MT, MST, IT, and area 7 of the parietal lobe (Bushnell *et al*. 1981; Moran & Desimone 1985; Motter 1994; Treue & Maunsell 1996; Luck *et al*. 1997), possibly extending back into striate cortex itself (Motter 1993). The extent to which non-target responses are suppressed—so that the network as a whole reflects only properties of the attended or target stimulus—depends very much on exact circumstances of the task and visual input, however. One important consideration is spatial separation of relevant and irrelevant inputs. Several studies have found far greater suppression of non-target responses when target and non-target both fall within the receptive field of the recorded cell (Moran & Desimone 1985; Treue & Maunsell 1996), implying that in many visual areas, much representation of non-targets remains across a whole cell population. Similarly, our IT results depend on the spatial layout of the display. If effective and ineffective stimuli lie on opposite sides of the visual meridian, we find that IT cells are driven not by the behaviourally relevant stimulus, but by whichever stimulus lies in the contralateral visual field (Chelazzi *et al*. 1998). A key consideration may be time. Early in the response, as we have seen, relevant and irrelevant inputs are equally represented in the neural signal (figure 6). The strongest suppression of non-target responses may take hundreds of milliseconds or more to develop (see, for example, Gottlieb *et al*. 1998; Motter 1994), as the appropriate selective state is established. An intriguing hypothesis is that factors such as spatial separation may be most important in an intermediate period between initial, strong non-target representation and final, substantial non-target suppression; a period that might be particularly important in studies whose stimuli last only a few hundred milliseconds.

7. CONCLUSION

Perhaps the key feature of the integrated competition hypothesis is its distributed view of attentional functions. Good examples are provided by several of the results I have described. Both our own lesion studies and others' results show how a lateral attentional imbalance arises from damage to many different brain areas. Our functional imaging studies suggest the joint involvement of prefrontal and occipital cortex in lateral attentional focus and competition. The single unit results suggest flexible involvement of several extrastriate systems in top-down attentional control by biased competition. More generally, 'attention' is seen as a widely distributed state, in which several brain systems converge to work on the different properties and action implications of the same, selected object.

Of course this framework has many points of uncertainty. In single unit studies, for example, it is clear that several factors influence competition for control of cellular responses, including proximity to the receptive field and side of visual space in addition to behavioural relevance. In a sense these factors reflect a failure of the network to integrate: when stimuli are widely separated, for example, different cells are dominated by different inputs. The strength of integration will also be a key factor in understanding the many reported dissociations in neglect, e.g. neglect restricted to one sensory modality (see, for example, Guariglia & Antonucci 1992). Although the tendency may be for different spatial systems to share a common dominant focus, this tendency is far from absolute. Already, however, we begin to see how three key concepts—competition, top-down control, and object integration—allow a coherent theoretical approach to the problem of visual attention from behavioural through to single unit levels.

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