NEURAL MECHANISMS OF SELECTIVE VISUAL ATTENTION

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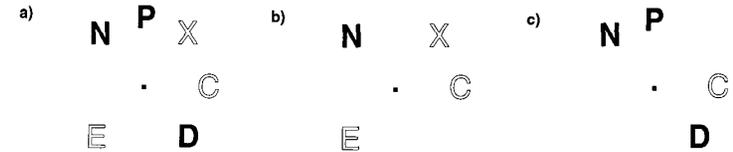KEY WORDS: vision, cortex, primates, visual search, neglect

Figure 1 Displays demonstrating limited processing capacity and selectivity in human vision. Subjects are shown the displays briefly and asked to report only the black letters. Limited capacity is shown by reduced accuracy as the number of targets is increased (compare *b* and *a*). Selectivity is shown by negligible impact of nontargets (compare *a* and *c*).

INTRODUCTION

The two basic phenomena that define the problem of visual attention can be illustrated in a simple example. Consider the arrays shown in each panel of Figure 1. In a typical experiment, before the arrays were presented, subjects would be asked to report letters appearing in one color (targets, here black letters), and to disregard letters in the other color (nontargets, here white letters). The array would then be briefly flashed, and the subjects, without any opportunity for eye movements, would give their report. The display mimics our usual cluttered visual environment: It contains one or more objects that are relevant to current behavior, along with others that are irrelevant.

The first basic phenomenon is limited capacity for processing information. At any given time, only a small amount of the information available on the retina can be processed and used in the control of behavior. Subjectively, giving attention to any one target leaves less available for others. In Figure 1, the probability of reporting the target letter N is much lower with two accompanying targets (Figure 1*a*) than with none (Figure 1*b*).

The second basic phenomenon is selectivity—the ability to filter out unwanted information. Subjectively, one is aware of attended stimuli and largely unaware of unattended ones. Correspondingly, accuracy in identifying an attended stimulus may be independent of the number of nontargets in a display (Figure 1*a* vs 1*c*) (see Bundesen 1990, Duncan 1980).

Taken together, such results suggest the following general model (Broadbent 1958; Neisser 1967; Treisman 1960, 1993). At some point (or several points) between input and response, objects in the visual input compete for representation, analysis, or control. The competition is biased, however, towards information that is currently relevant to behavior. Attended stimuli make demands on processing capacity, while unattended ones often do not.

In the following sections, we first outline the major behavioral characteristics of competition and consider the limitations within the nervous system that make competition necessary. We then describe selectivity, or how the competition may be resolved, at both the behavioral and neural level. To some extent, our account builds on early models of biased competition by Walley & Weiden (1973) and Harter & Aine (1984). The approach we take differs from the standard view of attention, in which attention functions as a mental spotlight enhancing the processing (and perhaps binding together the features) of the illuminated item. Instead, the model we develop is that attention is an emergent property of many neural mechanisms working to resolve competition for visual processing and control of behavior.

COMPETITION

Behavioral Data

In one simple type of experiment, two objects are presented in the visual field. Subjects must identify some property of both objects, with a separate response for each. Such studies reveal several important facts. First, dividing attention between two objects almost always results in poorer performance than focusing attention on one. Identifying simple properties of each object such as size, brightness, orientation, or spatial position gives much the same result as identifying more complex properties such as shape (see Duncan 1984, 1985, 1993).

A possible exception is simple detection of simultaneous energy onsets or offsets (Bonnel et al 1992).

Second, as long as the experiment uses brief stimulus exposures and measures the accuracy of stimulus identification, the major performance limitation appears to occur at stimulus input rather than subsequent short-term storage and response. For example, interference from processing two objects is abolished if they are shown one after the other, with an interval of perhaps a second between them (Duncan 1980), even though the two responses called for must still be remembered and made together at the end of the trial.

Third, interference is independent of eye movements. Even though gaze is always maintained at fixation, it is easier to identify one object in the periphery than two.

Fourth, interference is largely independent of the spatial separation between two objects, at least when the field is otherwise empty (Sagi & Julesz 1985, Vecera & Farah 1994). Though attention is sometimes seen as a mental spotlight illuminating or selecting information from a restricted region of visual space (Eriksen & Hoffman 1973, Posner et al 1980), performance seems not to depend on the absolute spatial distribution of information.

An enduring issue is the underlying reason for between-object competition. It has often been argued that full visual analysis of every object in a scene would be impossibly complex (Broadbent 1958, Tsotsos 1990). Competition reflects a limit on visual identification capacity. Equally strong, however, has been the view that competition concerns control of response systems (Allport 1980, Deutsch & Deutsch 1963). Certainly, some response activation often occurs from objects a person has been told to ignore (Eriksen & Eriksen 1974), which shows that unwanted information is not entirely filtered out in early vision. Very probably, competition between objects occurs at multiple levels between sensory input and motor output (Allport 1993).

Neural Basis for Competition

If the nervous system had unlimited capacity to process information in parallel throughout the visual field, competition between objects would presumably be necessary only at final motor output stages. Before discussing these motor stages, we first consider what limitations in the visual system make competition necessary at the input.

Objects in the visual field compete for processing within a network of 30 or more cortical visual areas (Desimone & Ungerleider 1989, Felleman & Van Essen 1991). These areas appear to be organized within two major cortico-cortical processing pathways, or streams, each of which begins with the primary visual cortex, or V1 (see Figure 2). The first, a ventral stream, is directed into the inferior temporal cortex and is important for object recognition, while the other, a dorsal stream, is directed into the posterior parietal cortex and is
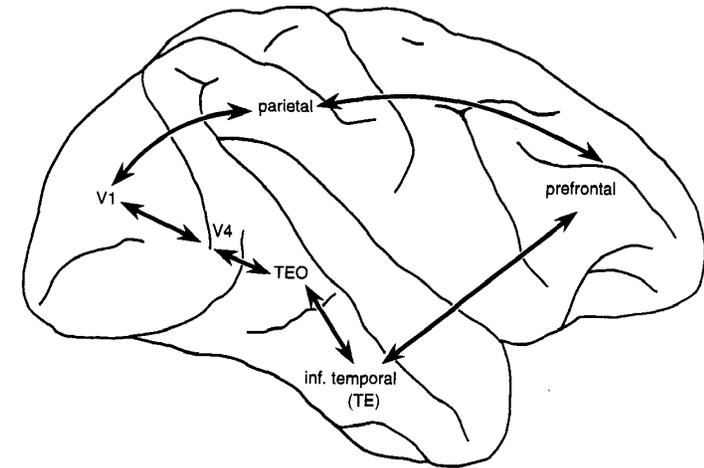

Figure 2 Striate cortex, or V1, is the source of two cortical visual streams. A dorsal stream is directed into the posterior parietal cortex and underlies spatial perception and visuomotor performance. A ventral stream is directed into the inferior temporal cortex and underlies object recognition. Both streams have further projections into prefrontal cortex. Adapted from Mishkin et al (1983) and Wilson et al (1993). For a "wiring diagram" of the areas and connections of the two streams, see Desimone & Ungerleider (1989) and Felleman & Van Essen (1991).

important for spatial perception and visuomotor performance (Ungerleider & Haxby 1994, Ungerleider & Mishkin 1982). Since competition impacts object recognition, we would expect to find one basis for it in the ventral stream.

The ventral stream includes specific anatomical subregions of area V2 (thin and interstripe regions), area V4, and areas TEO and TE in the inferior temporal (IT) cortex (see Desimone & Ungerleider 1989). As one proceeds from one area to the next along this pathway, neuronal properties change in two obvious ways. First, the complexity of visual processing increases. For example, whereas many V1 cells function essentially as local spatiotemporal energy filters, V2 neurons may respond to virtual or illusory contours in certain figures (von der Heydt et al 1984), and IT neurons respond selectively to global or overall object features, such as shape (Desimone et al 1984, Schwartz et al 1983, Tanaka et al 1991). Second, the receptive field size of individual neurons increases at each stage. As one moves from V1 to V4 to TEO to TE, typical receptive fields in the central field representation are on the order of 0.2, 3, 6, and 25° in size, respectively (see Boussaoud et al 1991, Ungerleider & Desimone 1989). Large receptive fields may contribute towards the recognition

of objects over retinal translation (Gross & Mishkin 1977, Lueschow et al 1994).

These receptive fields can be viewed as a critical visual processing resource, for which objects in the visual field must compete (Desimone 1992, Olshausen et al 1993, Tsotsos 1990). If one were to add ever more independent objects to a V4 or IT receptive field, the information available about any one of them would certainly decrease. If, for example, a color-sensitive IT neuron were to integrate wavelength over its large receptive field, one might not be able to tell from that cell alone if a given level of response was due to, say, one red object or two yellow ones or three green ones at different locations in the field. Such ambiguity may be responsible for the interference effects found in divided attention.

This ambiguity may be reduced, in part, by linking objects and their features to retinal locations. It is sometimes presumed that location information is absent from the ventral "what" stream altogether and must be supplied by the dorsal "where" stream. In fact, the ventral stream itself contains information about the retinal location of complex object features. V4 and TEO neurons process relatively sophisticated information about object shape (Desimone & Schein 1987, Gallant et al 1993, Tanaka et al 1991) and have retinotopically organized receptive fields (Boussaoud et al 1991, Gattass et al 1988). At any given retinotopic locus in these areas, receptive fields show considerable scatter. One could, in principle, derive information about the relative locations of nearby features from a population of cells with partially overlapping fields the same way one could derive information about a specific color from a population of neurons with broad but different color tuning. Similarly, although receptive fields in IT cortex may span 20–30 degrees or more, they are not homogeneous. Typically, the fields have a hot spot at the center of gaze, which may extend asymmetrically into the upper or lower contralateral visual field. Although the stimulus preferences of IT neurons remain the same over large retinal regions, for a large minority of cells the absolute response to a given stimulus changes significantly with retinal location, i.e. cells are tuned to retinal location the same way they are tuned to other object features (Desimone et al 1984, Lueschow et al 1994, Schwartz et al 1983; also see Chelazzi et al 1993a). Thus, in principle, objects and their locations might be linked to some extent within the ventral stream. Even so, parallel processing across the visual field is likely to be limited.

To sum up, retinal location, as with other object features, is coarsely coded in the ventral stream. Information about more than one object may, to some extent, be processed in parallel, but the information available about any given object will decline as more and more objects are added to receptive fields. Therefore, objects must compete for processing in the ventral stream, and the visual system should use any information it has about relevant objects to bias

the competition in their favor. This issue, which we term selectivity, is considered in later sections.

If the dorsal stream receives its visual input in parallel to the ventral stream as the anatomy suggests (Desimone & Ungerleider 1989), then it is presumably faced with competition among objects as well. As in IT cortex, receptive fields in posterior parietal cortex are very large, and it seems likely that increasing the number of independent objects in the visual field will eventually exceed the capacity of parietal cortex to extract the locations of each of them in parallel. Likewise, neural systems for visuomotor control must also deal with competition, to the extent that distractors are not already filtered out of the visual input (e.g. Munoz & Wurtz 1993a,b). Ultimately, for example, it is possible to move the eyes to only one target at a time. A critical issue is how selectivity is coordinated across the different systems so that the same target object is selected for perceptual and spatial analysis as well as for motor control.

SELECTIVITY: SCREENING OUT UNWANTED STIMULI

Behavioral Data

The ability to screen out irrelevant objects (Figure 1) is not absolute. It is easy in some cases and difficult in others, as is well illustrated in visual search. The subject detects or identifies a single target presented in an array of nontargets. Examples are shown in Figure 3. In easy cases, the target appears to "pop out" of the array, as if attention were drawn directly to it (Donderi & Zelnicker 1969, Treisman & Gelade 1980). Under such circumstances, the number of nontargets has little effect on the speed or accuracy of target detection or identification. In hard cases, however, nontargets are not filtered out well. In these instances, the number of nontargets in the display has a large effect on performance. An increase of 50 ms in target detection time for each nontarget added to the array is typical (Treisman & Gelade 1980), though in fact, this
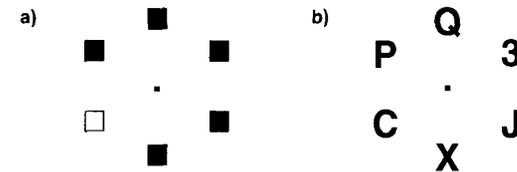
Figure 3 Selectivity in visual search. Target pop-out is revealed when the target is a mismatching element in an otherwise homogeneous field (*panel a*). Search is also extremely easy, however, whenever targets and nontargets are highly discriminable. Pop-out can also be based on more complex properties (*panel b*: search for the single digit).

figure varies widely and continuously from one task to another (Treisman & Gormican 1988).

According to the biased competition model, targets and nontargets compete for processing capacity in visual search. One factor influencing selectivity is bottom-up bias. It is very easy, for example, to find a unique target in an array of homogeneous nontargets (Figure 3a), perhaps reflecting an enduring competitive bias towards local inhomogeneities (Sagi & Julesz 1984). There may be similar biases towards sudden appearances of new objects in the visual field (Jonides & Yantis 1988) and towards objects that are larger, brighter, faster-moving, etc (Treisman & Gormican 1988).

An attentional system, however, would be of little use if it were entirely dominated by bottom-up biases. What is needed is a way to bias competition towards whatever information is relevant to current behavior. That is, one needs top-down control in addition to bottom-up, stimulus-driven biases. Correspondingly, there are many cases of easy search that do not depend on local inhomogeneity or sudden target onset. A colored target in a multicolored display, for example, may show good pop-out if the colors are highly discriminable (Duncan 1989). At least after a little practice, pop-out can be obtained during search for a single digit among letters (Figure 3b) (see Egeth et al 1972, Schneider & Shiffrin 1977).

Even when target selection is guided by top-down control, the ability to find targets is still dependent on bottom-up stimulus factors, especially the visual similarity of targets to nontargets. Provided that targets and nontargets are sufficiently different, however, easy search can be based on many different visual attributes, including simple features, such as size or color, and more complex conjunctions of these features (Duncan & Humphreys 1989, McLeod et al 1988, Wolfe et al 1989). Conjunction search provides a good example of the importance of similarity. In Figures 4a and b, the target is a large, white vertical bar. This target is much harder to find in Figure 4a, where each nontarget shares two properties with the target, than in Figure 4b, where only one property is shared (Quinlan & Humphreys 1987). Indeed, the latter case can give excellent pop-out; a similar result can be produced simply by increasing the discriminability of each conjunction's component features (Wolfe et al 1989).

Such results suggest the following model of biased competition. According to the task, any kind of input—objects of a certain kind, objects with a certain color or motion, objects in a certain location, etc—can be behaviorally relevant. Some kind of short-term description of the information currently needed must be used to control competitive bias in the visual system, such that inputs matching that description are favored in the visual cortex (Bundesen 1990, Duncan & Humphreys 1989). This short-term description has been called the attentional template (Duncan & Humphreys 1989): it may be seen as one aspect
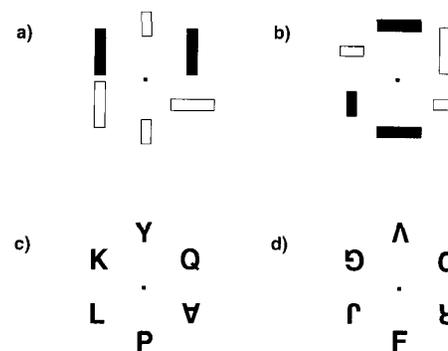

Figure 4   (a, b) Discriminability between targets and nontargets in conjunction search. Searching for a large, white vertical bar is harder when nontargets share two (panel a) rather than one (panel b) property with the target. In the latter case good pop-out can be obtained. (c, d) Novelty bias. It is easier to find a single inverted letter among upright nontargets (panel c) than the reverse (panel d).

of working memory (Baddeley 1986). The template can specify any property of required input—shape, color, location, etc.

Visual search is easy if targets and nontargets are easily discriminable. In this case, nontargets are poor matches to the attentional template and receive a weak competitive bias. Thus, the time it takes to find the target may be independent of the number of nontargets in the display. By contrast, search is difficult if nontargets are similar to the target. In this case, the competitive advantage of the target is reduced because each nontarget shares in the bias provided by the attentional template. Thus, each nontarget added to the display interferes with target detection. Alternative, serial-search accounts are considered below.

A great deal of work has dealt specifically with spatial selection, i.e. selection based on some cue to the location of target information (Eriksen & Hoffman 1973, Posner et al 1980, Sperling 1960). Indeed, spatial selection is often dealt with as a special case. We do not review this work in detail; it was covered earlier by Posner & Petersen (1990), and Colby (1991) has reviewed the neural mechanisms of spatial selection. Certainly, however, space is only one of the many cues that can be used in efficient target selection. A general account of selectivity must deal with both spatial and nonspatial cases. In terms of the biased competition model, prior knowledge of the target's spatial location is just another type of attentional template that can be used to bias competition in favor of the target.

A final consideration is bias derived from long-term memory. One interest-

ing case is bias to novelty. As shown in Figures 4c and d, for example, it is much easier to find an inverted (novel) target among upright (familiar) non-targets (Figure 4c) than the reverse (Figure 4d) (Reicher et al 1976). In fact, the time it takes to find an inverted character may be independent of the number of upright ones in a display (Wang et al 1992), which implies that multiple objects have parallel access to memory and that familiarity is a type of object feature that can be used to bias attentional competition. A second consideration is long-term learned importance. In a busy room, attention can be attracted by the sound of one's own name spoken nearby (Moray 1959). Similarly, long practice with one set of visual targets makes them hard to ignore when they are subsequently made irrelevant (Shiffrin & Schneider 1977). Thus, the top-down selection bias of a current task can sometimes be overturned by information of long-term or general significance acting in a bottom-up fashion. In the next sections we consider both bottom-up and top-down mechanisms for resolving competition.

Bottom-Up Neural Mechanisms for Object Selection

The first neural mechanisms for resolving competition we consider are those that derive from the intrinsic or learned biases of the perceptual systems towards certain types of stimuli. We describe them here as bottom-up processes, not because they do not involve feedback pathways in visual cortex (they may well do so) but because they appear to be largely automatic processes that are not dependent on cognition or task demands.

Stimuli that stand out from their background are processed preferentially at nearly all levels of the visual system. In visual cortex, the responses of many cells to an otherwise optimal stimulus within their classically defined receptive field may be completely suppressed if similar stimuli are within a large surrounding region (for reviews see Allman et al 1985, Desimone et al 1985). The greater the density of stimuli in the surround, the greater the suppression (Knierim & Van Essen 1992). In the middle temporal area (MT), for example, a cell that normally responds to vertically moving stimuli within its receptive field may be unresponsive if the same stimuli are part of a larger moving pattern covering the receptive field and surround (Allman et al 1985, Tanaka et al 1986). These mechanisms almost certainly contribute to the pop-out effects of targets in visual search.

As indicated above, the visual system also seems to be biased towards new objects or objects that have not been recently seen. Thus, the temporal context of a stimulus may contribute as much to its saliency as its spatial context. In the temporal domain, stimuli stored in memory may function as the temporal surround, or context, against which the present stimulus is compared.

Striking examples of such temporal interactions have been found in the anteroventral portion of IT cortex. Most studies in this region recorded cells

while monkeys performed delayed matching-to-sample (DMS) tasks with either novel or familiar stimuli. In DMS, a sample stimulus is followed by one or more test stimuli, and the animal signals when a test stimulus matches the sample. For up to a third of the cells in this region, responses to novel sample stimuli become suppressed as the animal acquires familiarity with them (Fahy et al 1993, Li et al 1993, Miller et al 1991, Riches et al 1991). The cells are not novelty detectors, in that they do not respond to any novel stimulus. Rather, they remain stimulus selective both before and after the visual experience.

In fact, this shrinkage in the population of activated neurons as stimuli become familiar may increase the selectivity of the overall neuronal population for those stimuli. As one learns the critical features of a new stimulus, cells activated in a nonspecific fashion drop out of the activated pool of cells (Li et al 1993), leaving those that are most selective. There is also direct evidence that some IT cells selective for faces become more tuned to a familiar face following experience (Rolls et al 1989).

An effect akin to the novelty effect is also found for familiar stimuli that have been seen recently. When a test stimulus matches the previously seen sample in the DMS trial, responses to that stimulus tend to be suppressed (Miller et al 1991, 1993; also see Baylis & Rolls 1987, Eskandar et al 1992, Fahy et al 1993, Riches et al 1991). Although it was originally proposed that this suppressive effect was dependent on active working memory for the sample, recent work has shown it to be an automatic outcome of any stimulus repetition (Miller & Desimone 1994). For many cells, this suppression occurs even if the repeated stimuli differ in size or appear in different retinal locations (Lueschow et al 1994). Thus, the detection of novelty and recency apparently occurs at a high level of stimulus representation.

Taken together, the results indicate that both novel stimuli and stimuli that have not been recently seen will have a larger neural signal in the visual cortex, giving them a competitive advantage in gaining control over attentional and orienting systems. This would explain the bias towards novelty in the human behavioral data described above. The longer the organism attends to the object, the more knowledge about the object is incorporated into the structure of the cortex; this reduces the visual signal. It will also reduce the drive on the orienting system so that the organism is free to orient to the next new object (Li et al 1993, Desimone et al 1994). This view is compatible with Adaptive Resonance Theory (Carpenter & Grossberg 1987), in which novel stimuli activate attentional systems that allow new long-term memories to be formed. Consistent with these neurophysiological results in animals, a reduction in neural activation with stimulus repetition in human subjects has been seen in both event-related potentials of the temporal cortex (Begleiter et al 1993) and in brain-imaging studies (Squire et al 1992).

Top-Down Control of Selection in the Ventral Stream

As we have said, top-down biases on visual processing, or the attentional template, derive from the requirements of the task at hand. Although we consider mechanisms for spatial and object selection separately, they in fact share many features.

SELECTION BASED ON SPATIAL LOCATION   As we described above, one central resource for which stimuli compete in the ventral stream seems to be the receptive field. Not surprisingly then, spatial selection in this stream does not simply enhance processing of the stimulus at the attended location but rather seems to resolve competition between stimuli in the receptive field.

In one study of cells in V4 and IT cortex, monkeys performed a discrimination task on target stimuli at one location in the visual field, ignoring simultaneously presented distractors at a second location (Moran & Desimone 1985). The target location for a given run was indicated to the monkey by special instruction trials at the start of that run, i.e. the spatial bias was purely top down and presumably required spatial working memory. When target and distractor were both within the receptive field of the recorded cell, the neuronal response was determined primarily by the target; responses to the distractor were greatly attenuated. The cells responded as though their receptive fields had shrunk around the target. Consistent with this, Richmond et al (1983) found that the presence of a central fixation target in the receptive field of an IT neuron may block the response to a more peripheral stimulus in the field.

In the Moran & Desimone (1985) study, when one of the two locations was placed outside the receptive field of the recorded cell, attention no longer had any effect on the response. This was consistent with the biased competition model: Target and distractor were no longer competing for the cell's response, and thus, top-down spatial bias no longer had any effect.

Receptive fields and the region of space over which attention operated were much larger in the IT cortex. However, even here attentional effects were larger when target and distractor were located within the same hemifield and, therefore, more likely to be in competition (Sato 1988).

In V1, receptive fields were too small to test the effects of placing both target and distractor within them. However, when one stimulus was located inside, and one outside (at the same spatial separation used in area V4), there was no effect of attention on V1 cells in this paradigm. These results suggest that target selection is a two-stage process: The first stage works over a small spatial range in V4, and the second stage works over a much larger spatial range in IT cortex; both are in line with their receptive field sizes (Moran & Desimone 1985). Studies of event-related potentials in humans have also

localized a region modulated by spatial attention in lateral prestriate cortex; this region may correspond to area V4 (Mangun et al 1993).

Recently, Motter (1993) has reported attentional effects on responses of cells in V1, V2, and V4. In contrast to the Moran & Desimone (1985) study, these effects were found when one stimulus was inside the field, and others outside. Most surprisingly, cueing the animal for the target location was almost as likely to suppress responses to the target as to facilitate them. A possible reason for the discrepancy between the two studies is that Motter (1993) found these effects only when there were a large number of distractors in the visual field, whereas Moran & Desimone (1985) used only a single distractor. Increasing the competition among objects in the visual field may have increased the role of attentional biases. Other differences include the fact that Motter used an explicit spatial cue to indicate the target location in the display, and the target (but not any of the distractors) was physically added to the cue, possibly inducing some complex sensory effects. In any event, other recent studies have confirmed that attentional effects in V4 are much larger when target and distractor compete within the same receptive field than in any other configuration (Luck et al 1993; L Chelazzi, unpublished data).

CIRCUITRY UNDERLYING SPATIAL SELECTION   Although the synaptic mechanisms mediating the gating of V4 and IT responses are unknown, anatomy dictates that they fall into either of two classes (Desimone 1992). In the first class, spatial biasing inputs to visual cortex determine which specific subset of a cell's inputs causes the cell to fire, whereas in the second class, the inputs determine which specific cells in a population are allowed to fire. In other words, one can either gate some of the inputs to a cell on or off, or one can gate some of the cells on or off. Theoretical models for both classes of circuitry have been developed (Anderson & Van Essen 1987, Crick & Koch 1990, Desimone 1992, Niebur et al 1993, Olshausen et al 1993, Tsotsos 1994). All of the models resolve competition when there are mulitple stimuli within the receptive field. Presently, there are insufficient data to decide between them.

If the gating of V4 and IT responses occurs as a result of an external input that biases competition in favor of the target, one might expect to see some evidence for it. A possible candidate has been found in a new study of spatial attention in V4 (Luck et al 1993). V4 cells in this study showed a sustained elevation of their baseline (prestimulus) firing rates whenever the animal's attention was directed inside their receptive field. This elevation of activity with attention could be the neural analogue of the attentional template for location. The elevation occurred at the start of each trial before any stimulus had appeared. Since the only information about where to attend was given to the animal minutes earlier at the start of a block of trials, the relevant location must have been stored in working memory. The spatial resolution of this source

was very high; when attention was shifted to different regions within the same receptive field, the magnitude of the baseline shift varied according to the distance between the focus of attention and the receptive field center. Thus, whatever spatial bias signal enters the cortex, it apparently has a spatial resolution finer than the receptive field dimensions of V4 cells.

SELECTION BASED ON FEATURES   The mechanism underlying the selection of objects by their features (when their location is not known in advance) requires a means to hold the sought-after object in working memory and to use this memory (or attentional template) to resolve competition among the elements in the scene. Recently, evidence for this selection mechanism has been found in the anteroventral portion of IT cortex, the same portion in which memory-related activity has been found (Chelazzi et al 1993a).

Monkeys were briefly presented with a complex picture (the cue) at the center of gaze to hold in memory. The cue on a given trial was either a good stimulus that elicited a strong response from the cell or a poor stimulus that elicited little or no response when presented by itself. Following a delay, the good and the poor stimuli were both presented simultaneously as choice stimuli, at an extrafoveal location. The monkey made a saccadic eye movement to the target stimulus that matched the cue, ignoring the nonmatching stimulus (the distractor).

As shown in Figure 5, the choice array initially activated IT cells tuned to the properties of either stimulus, in parallel, irrespective of which stimulus was the target. Within 200 ms after array onset, however, the response changed dramatically depending on whether the animal was about to make an eye movement to the good or poor stimulus. When the target was the good stimulus, the response remained high. However, when the target was the poor stimulus for the recorded cell, the response to the good distractor stimulus was suppressed even though it was still within the receptive field. This change in response occurred about 100 ms before the onset of the eye movement. The cells responded as though the target stimulus captured their response, so neuronal activity in IT cortex reflected only the target's properties. Cells selective for the nontargets were suppressed within 200 ms and remained suppressed until well after the eye movement was made. Similar effects were found for choice arrays of larger sizes.

Just as with spatially directed attention, these effects of object selection in the IT cortex were much smaller when target and nontargets were located in opposite hemifields than when they were in the same hemifield, i.e. when they were maximally in competition. Interestingly, similar competitive effects are seen even at high levels of oculomotor control in the frontal eye field. Cells in this region were recorded while monkeys made eye movements to a target in a field of distractors (Schall & Hanes 1993). Responses to distractors in the
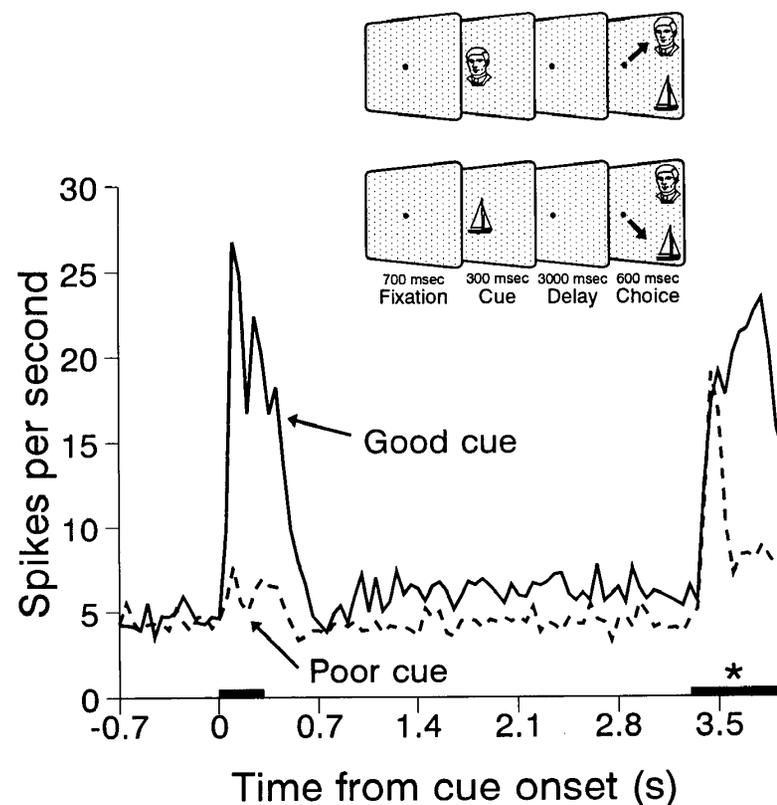
Figure 5 Effects of object selection on responses of cells in the IT cortex. The upper insert illustrates the general visual search task. Graphs show the average response of 22 cells recorded while monkeys performed the task. The cue was chosen to be either a good or a poor stimulus for the recorded cell. When the choice array was presented, the animal made a saccadic eye movement to the stimulus (target) that matched the previous cue. The saccadic latency was 300 ms, indicated by the asterisk. Cells had a higher firing rate in the delay preceding the choice array when their prefered stimulus was the cue. Following the delay, cells were activated (on the average) by their prefered stimulus in the array, regardless of whether it was the target. However, 100 ms before the eye movement was made, responses diverged depending on whether the target was the good or the poor stimulus. The two dark horizontal bars indicate when the cue and the choice were presented. Adapted from Chelazzi et al (1993a).

receptive field were more suppressed when the competing target was located just outside the receptive field, and thus maximally competitive, than when it was further away.

Two findings suggest that the target is selected in the IT cortex as a result

of inputs (initiated at the time of the cue) that bias competition in favor of the target. First, IT cells selective for the properties of the cue-target show higher maintained activity in the delay following the cue than do cells selective for the distractor. This could be the neural correlate of the attentional template for the target. Second, a subpopulation of the cells gives enhanced responses to the choice array when their preferred stimulus is the target, even during the first 200 ms in which all cells tend to be active. Together, the results indicate that cells selective for the target are primed to respond to it by an external source before the onset of the choice array; they then give an enhanced response to the target when it appears. Eventually, as a result of competitive interactions during the initial visual activation, cells selective for the distractors are suppressed. At some point in time, mechanisms for spatial selection may also be engaged to facilitate localization of the target for the eye movement.

Cue-, or template-, related activity during delay periods (Fuster & Jervey 1981, Miller et al 1993, Miyashita & Chang 1988) and enhanced responses to (target) stimuli matching a prior cue (Miller & Desimone 1994) have also been found in studies of working memory in IT cortex. Visual search simply appears to be a variant of a working memory task, in which the distractors are distributed in space rather than time. Importantly, the same seems to be true of spatial selection, which shares many features with object selection, including template-related activity during delays followed by response-suppression to competing nontargets. The major difference may simply be the nature of the template. The potential sources of the template that primes IT cells in working memory is considered below.

Somewhat similar mechanisms may be reflected in studies of human brain activation that use positron emission tomography (PET). In one study (Corbetta et al 1991), subjects were asked to compare one feature of two successive displays, each containing a moving field of colored shapes. Different portions of extrastriate cortex were preferentially activated depending on whether the relevant feature was motion, on the one hand, or color or shape, on the other. Physiological studies have also shown a variety of other nonspatial, top-down influences on ventral stream neurons that may influence object selection bias, but they are beyond the scope of this review (e.g. Maunsell et al 1991, Spitzer et al 1988, Spitzer & Richmond 1991).

Neural Sources of Spatial Selection Bias

LESION STUDIES IN HUMANS   We now turn to the neural systems that might be the source of the attentional template for spatial location. The lesion data are readily explained by the biased competition model but, unfortunately, do not by themselves pin down the critical sources.

Following the formation of a lesion on one side of the brain, there is often

a disregard or neglect of objects and actions in contralateral space (for review see Bisiach & Vallar 1988). Neglect can be manifested as failure to copy one half of a drawing, to read text on one half of a page, to shave one half of the face, etc.

Neglect of one form or another has been associated with damage to a great variety of brain structures, including the parietal cortex (e.g. Bisiach & Vallar 1988), the frontal cortex (Heilman & Valenstein 1972), the cingulate gyrus (Watson et al 1973), the basal ganglia (Hier et al 1977), the thalamus (Rafal & Posner 1987, Watson & Heilman 1979), the midbrain and superior colliculus (Posner et al 1982), and even the temporal lobe (Shelton et al 1990).

Most importantly, neglect of the contralesional side can be exaggerated by competing events on the other, unimpaired, side—a phenomenon termed extinction. Thus, neglect manifests more as a competitive bias against one side than as an absolute inability to deal with that side (Kinsbourne 1993). If there are critical spatial gating inputs to the ventral stream, they probably arise from more than one structure.

In terms of the biased competition model, damage to the spatially mapped areas of one hemisphere may cause two different types of behavioral impairment. First is the loss of whatever functions are mediated by the damaged areas, which may include perceptual, visuospatial, and oculomotor functions. Second is the loss of competitive weights afforded to objects in the affected portion of the contralesional field, which may be manifested anywhere between sensory input and motor output. In the visual system, this loss could affect visual cortex either directly, through the elimination of structures that contribute to stimulus saliency or that supply top-down spatial selection inputs, or indirectly, through the elimination of structures that supply the critical ones with inputs. The superior colliculus does not project directly to the visual cortex, for example, but ultimately provides inputs to other structures that do. Either unilateral or focal damage to the colliculus could affect competition within these other parts of the system, thus throwing them out of balance (Desimone et al 1990b). A loss of competitive weights would also explain why neglect and extinction most commonly follow unilateral rather than bilateral lesions; with bilateral lesions, neither hemifield has a competitive advantage over the other. It seems likely that competition in multiple brain systems is coordinated so that a loss of competitive weights in one system has general effects in others.

Considering that lesions will typically result in both a loss of function and a loss of competitive weights and that competitive weights may be affected at any level between sensory input and motor output, it is not surprising that there are many reports of dissociation between one form of neglect and another. For example, there are reports of neglect of body vs environmental objects (e.g. Guariglia & Antonucci 1992), neglect of close vs far space (e.g. Halligan &

Marshall 1991), and sensory vs motor neglect (e.g. Tegner & Levander 1991). There are also strong laterality effects, which we do not cover here (see Posner & Peterson 1990).

One interesting possibility raised by lesion studies is that the posterior parietal cortex specifically mediates disengaging attention from its current focus (Posner et al 1984), or in our terms, shifting the balance of competitive weights from one object to another. A disengagement deficit may partly explain rare cases of Balint's syndrome and simultagnosia following extensive bilateral damage to the parietal lobe (e.g. Humphreys & Riddoch 1993). In these patients, attention can become locked onto one object; nonattended objects seem to disappear. According to Posner and colleagues, this disengage function of the parietal cortex differs from that of the superior colliculus and pulvinar, which they propose mediate moving attention and focusing attention, respectively (reviewed in Posner & Petersen 1990). This division is based primarily on reaction time data from patients with large unilateral lesions affecting, but generally not limited to, one of the three structures. However, monkeys with discrete unilateral lesions or deactivation of any one of these structures all show a general slowing of reaction times for targets in the contralesional field as well as a disengagement impairment when attention is switched from the ipsilesional to contralesional field (see below). These impairments may simply follow from a loss of competitive weights in the affected field. Thus, a specific role for parietal cortex in disengagement is still an open question.

LESION STUDIES IN PRIMATES   The general rule for lesion effects in monkeys is the same as in humans: Unilateral lesions of structures with a contralateral field representation result in a loss of whatever functions are mediated by the damaged area as well as neglect and extinction syndromes from a loss of competitive weights in the contralesional field. Bilateral lesions, which do not upset the competitive balance between the fields, tend to have less effect on spatial attention.

In fact, there are at least two instances when adding a lesion in one hemisphere corrects an attentional impairment caused by a lesion in the other. Monkeys with unilateral lesions of the posterior parietal cortex tend to make voluntary eye movements into the ipsilesional field when presented with bilateral stimuli. However, this bias is corrected when an additional lesion is subsequently made in the posterior parietal cortex of the opposite hemisphere (Lynch & McLaren 1989). Similarly, cats with unilateral lesions of striate cortex show a severe contralateral neglect; however, a lesion of the substantia nigra in the opposite hemisphere substantially reduces the neglect (Wallace et al 1990).

PULVINAR   The most frequently proposed source of attentional inputs to the cortex has probably been the pulvinar (e.g. see Crick 1984, Olhausen et al

1993). This large structure contains several different nuclei, each of which contains one or more functionally distinct regions connected anatomically to a specific region of the visual cortex (Bender 1981; Benevento & Rezak 1976; Ungerleider et al 1983, 1984). The pulvinar has been implicated in attentional control based on neuropsychological studies of humans with thalamic brain damage (Rafal & Posner 1987), PET activation studies (LaBerge & Buchsbaum 1990), and physiological recording and chemical deactivation studies in monkeys (Desimone et al 1990b; Petersen et al 1985, 1987; Robinson et al 1986). However, pulvinar lesions raise the same issues of interpretation as lesions in other structures we have considered.

In one study, the portion of the pulvinar termed Pdm, which is anatomically interconnected with the posterior parietal cortex, was reversibly deactivated in one hemisphere (Petersen et al 1987). Following deactivation, reaction times to targets in the contralesional field were slower than normal, especially when attention was first misdirected into the ipsilesional field (i.e. a disengage impairment). Thus, Pdm deactivation seemed to reduce the saliency of contralesional stimuli thereby reducing their competitive weights for either visual processing or control over behavior (Robinson & Petersen 1992). This loss of weights may have simply resulted from the loss of Pdm inputs to the posterior parietal cortex of the same hemisphere, as the latter structure is implicated in attentional control in its own right (see below). Both unilateral deactivation of the superior colliculus and unilateral lesions of the posterior parietal cortex had effects similar to those of Pdm deactivation (see Colby 1991).

Analogous results were found with unilateral chemical deactivation of the lateral pulvinar (PL), the part connected with areas V4 and IT cortex. Monkeys discriminated the color of a target in the (contralesional) field opposite the deactivated pulvinar, with or without a distractor in the unaffected (ipsilesional) field (Desimone et al 1990b). The deactivation had no effect on the monkey's ability to discriminate the target unless it was paired with a distractor, a result reminiscent of extinction. If PL was the source of critical gating inputs to extrastriate cortex, moving the distractor closer to the target should have had a devastating effect on performance. However, when the distractor was moved into the same hemifield as the target, the impairment was substantially diminished, presumably because neither stimulus then had a competitive advantage. As with Pdm, deactivation of PL most likely deprived visual cortex in the same hemisphere of excitatory inputs and reduced target saliency. Bilateral pulvinar lesions have no effect on the ability of monkeys to find a target embedded in distractors, which further suggests that PL does not have a necessary role in attentional gating (Bender & Butter 1987).

In fact, the biased competition model predicts results similar to those of pulvinar deactivation from partial lesions in any spatially mapped visual structure that makes a contribution to saliency and hence competitive weight. Such

an outcome is observed in monkeys with lesions affecting one quadrant of the visual field representation in area V4. In one study, animals were trained to make eye movements to an odd-man-out target in an array of stimuli presented around an imaginary ring (Schiller & Lee 1991). If the target was located in the lesion quadrant and if it was dimmer than the other stimuli in the unaffected parts of the field, the animals were impaired. However, there was no impairment if the target was brighter than the other stimuli, suggesting that the V4 lesion reduced target saliency. In another study, animals were especially impaired in discriminating the shape of a target located in the lesion quadrant when a distractor was located in an unaffected part of the field; however, there was little impairment when both the target and distractor were located within the lesion quadrant (Desimone et al 1990a). In the latter configuration, neither stimulus had a competitive advantage from the lesion.

In summary, the biased competition model affords a ready explanation for the effects of unilateral or partial lesions on attention. At this time, the pulvinar is no more likely than other structures to be a critical source of gating inputs to the ventral stream. To pin down these sources will likely require converging evidence from lesion and physiological studies.

PHYSIOLOGICAL STUDIES   The classic paradigm for studying cells within the presumed control system for spatial attention has been the saccadic enhancement paradigm (Goldberg & Wurtz 1972, Wurtz & Goldberg 1972). In this task, the monkey fixates a central stimulus while a second stimulus is presented within a cell's receptive field in the periphery. In the experimental condition, the fixation stimulus is turned off and the animal saccades to the receptive field stimulus when it appears. In a control condition, the fixation stimulus stays on and the monkey is rewarded for signaling when it dims, ignoring the receptive field stimulus. The control over eye movements is largely top down in this task, although the experimental condition has some automatic, or reflexive, components.

Some of the cells in virtually all structures implicated in spatial attention give larger responses to the receptive field stimulus in the experimental condition (the target) than in the control (the distractor), a result usually termed the enhancement effect (although, in fact, it is often unclear whether the target response is enhanced or the distractor response is suppressed). This effect is found in the superior colliculus, the substantia nigra, the Pdm nucleus of the pulvinar, the posterior parietal cortex, the frontal eye fields (Goldberg & Wurtz 1972, Hikosaka & Wurtz 1983, Lynch et al 1977, Robinson et al 1978, Petersen et al 1985, Wurtz & Mohler 1976; also see Colby 1991), and the dorsolateral prefrontal cortex (di Pelligrino & Wise 1993b). However, in both the superficial layers of the colliculus and the frontal eye fields, the effect is known to be specific for saccadic eye movements; no enhancement is found when the

animal simply attends to the peripheral stimulus and signals when it dims by releasing a bar (Colby et al 1993, Goldberg & Bushnell 1981, Wurtz & Mohler 1976). Thus, these cells appear to be involved in the selection of targets for eye movements rather than in selection for visual processing. A remarkable implication of the fact that these visuomotor cells respond equally to targets and distractors in the absence of eye movements is that visual input to these parts of the oculomotor system does not derive from cells in the dorsal and ventral streams whose responses are gated by spatial attention. Competition between stimuli must take place independently within the oculomotor system and yet be coordinated with competition within visual processing systems.

Although cells in the substantia nigra and intermediate layers of the colliculus have not yet been tested in this condition of attention without eye movements, cells in Pdm, dorsolateral prefrontal cortex, and posterior parietal cortex all show the enhancement effect in this purely attentional condition (Bushnell et al 1981, Colby et al 1993, di Pelligrino & Wise 1993b, Petersen et al 1985). Of these three regions, the posterior parietal and prefrontal cortices may be the most critical for spatial attention, as the enhancement in Pdm may simply reflect the input it receives from the posterior parietal cortex. Furthermore, studies with PET have shown activation of posterior parietal cortex in a task involving shifting attention (Corbetta et al 1993). Thus, based on presence of the enhancement effect, both posterior parietal and prefrontal cortex are possible sources of a spatial-biasing signal to visual cortex.

If the top-down selection of spatial locations for attention typically involves working memory, as we have suggested, an important clue to the identity of the relevant cells would be response activation in working memory tasks. In fact, in such tasks cells in the dorsolateral prefrontal and posterior parietal cortexes are tonically active whenever the animal holds "in mind" a location within a cell's receptive field (in the absence of any stimulus) (Chelazzi et al 1993b, Colby et al 1993, di Pelligrino & Wise 1993a, Funahashi et al 1989, Fuster 1973, Gnadt & Andersen 1988, Quintana & Fuster 1992, Wilson et al 1993). Furthermore, these two regions are heavily interconnected anatomically and appear to form part of a distributed system for spatial cognition (for a review, see Goldman-Rakic 1988). These physiological data, in conjunction with data showing neglect and extinction effects following both prefrontal and posterior parietal lesions, argue that both structures may work together in generating top-down spatial selection biases.

Sources of Object Selection Bias

As with spatial selection, the attentional templates for objects and their features may derive from mechanisms underlying working memory. If so, then the prefrontal cortex most likely plays an important role. Just as lesions of the dorsolateral prefrontal cortex impair working memory for space (see Funahashi

et al 1993), lesions of the ventral prefrontal cortex impair working memory for objects (Mishkin & Manning 1978). Furthermore, Wilson et al (1993) report that cells in the dorsolateral cortex have maintained activity for object location whereas cells in the ventral cortex have maintained activity for object identity. Indeed, the dorsal and ventral prefrontal cortices appear to be the frontal extensions of the dorsal and ventral processing streams, respectively (Mishkin et al 1983, Wilson et al 1993).

Just as the posterior parietal cortex may work together with the dorsolateral prefrontal cortex in generating spatial templates, the anterior IT cortex may play an analogous role with the inferior prefrontal cortex in generating object and feature templates (Desimone et al 1994, Fuster et al 1985). Both are heavily interconnected anatomically (Ungerleider et al 1989), and neurons in both structures are activated during identical working memory tasks for objects (Chelazzi et al 1993b).

OBJECTS, GROUPING, AND THE BINDING PROBLEM

So far we have not dealt specifically with the representation of objects in the cortex. Although this is a key issue for understanding attention, little is actually known about the neural representations of objects. We review just a few of the relevant behavioral and neurophysiological facts.

As described above, when human subjects divide attention between two objects, the decrement in performance is rather insensitive to spatial separation. What does matter in divided attention is whether two properties to be identified belong to the same or different objects. It is far easier to identify two properties (e.g. orientation and contrast) of one object than properties of two different objects (Duncan 1993, Lappin 1967), even when the two objects overlap (Duncan 1984). Indeed, under simple conditions subjects can identify two properties of a single object just as easily as they can identify one (Duncan 1984, 1993).

The operations that segment and group visual input into discrete objects or chunks are beyond the scope of this review. Many factors combine to determine which parts of the visual input belong together, including spatial proximity, shared motion or color, contour features such as local concavities and T-junctions, and long-term familiarity with the object (see e.g. Beck et al 1983, Hummel & Biederman 1992, Grossberg et al 1994, Palmer 1977). The data suggest, however, that the objects so constructed behave as wholes when they compete for visual representation and/or control of behavior.

Strengthening the perceived grouping between irrelevant and relevant display items by, for example, giving them a common motion makes the irrelevant items harder to ignore (Driver & Baylis 1989, Kramer & Jacobson 1991). The ease of visual search in homogenous arrays (Figure 3a) partly reflects the

tendency of identical nontargets to group together and apart from the target. Visual grouping determines which parts of the input belong together; subsequent competitive operations tend to respect, or preserve, these groupings (Duncan & Humphreys 1989).

Other than a general tendency for neuronal responses in the visual cortex to be influenced by the overall distribution of items within the receptive field, the neural mechanisms underlying object grouping are unknown. Grossberg et al (1994) have attempted to model grouping as a product of mechanisms for image segmentation. Given the importance of grouping for attentional control, this is a ripe area for future research.

Closely related to grouping is the binding problem, or the problem in a distributed representation of keeping together parts or attributes of the same object or entity (Hinton & Lang 1985). It is often presumed that there are separate representations for different features, such as color and orientation, in the cortex. If so, then an obvious question is how the color red, say, becomes bound to the bar of the appropriate orientation when there are multiple colored bars of different orientation in the visual field. A common view is that attention helps solve the binding problem by linking together different features at the attended location (Treisman & Gelade 1980, Treisman & Schmidt 1982). One problem with this view is that a complex object such as a face has many different features that would need to be bound together, one at a time. Multipart objects, such as the human body, may have hierarchical part-whole relationships that would require comparable binding hierarchies (e.g. a finger may be seen as part of a hand, a limb, or the entire body). Additionally, as we have said, targets may pop out of a visual search display before they are the focus of attention, even when they are defined by the conjunction of elementary attributes (Duncan & Humphreys 1989, McLeod et al 1988, Wolfe et al 1989). This implies some type of solution to the binding problem that works in parallel across the visual field.

At the neural level, the necessity to bind together the output of cells specialized for different elemental features may be overstated. To our knowledge, no cortical cell has ever been reported that is influenced by only one stimulus feature. Neurons may convey more information about some features than others, but their responses often vary along many different feature dimensions, particularly in area V4 and IT cortex (Desimone et al 1984, Tanaka 1993). Some cells in temporal cortex respond specifically to objects with highly complex conjunctions of features, such as faces, even under anesthesia when selective attention is presumably absent (Desimone et al 1984). A possible role for correlated activity of neurons in binding is considered elsewhere in this volume (Singer & Gray 1995). As with grouping, much more needs to be known about object representations in the cortex before we understand the role of attention in binding.

SERIAL AND PARALLEL MODELS

When targets are selected by spatial location, all models of the underlying mechanism posit some type of spatial gating mechanism. It is when the target's location is unknown and it must be found on the basis of its identity (e.g. searching for a face in a crowd) that different classes of models diverge significantly. According to serial search accounts, scenes are searched element by element by a spotlight of attention (Olhausen et al 1993, Schneider & Shiffrin 1977, Treisman & Gelade 1980), unless the target pops out from the background on the basis of an elemental feature difference. As each element is selected in turn by attention, it is evaluated by a recognition memory process, and the scan of the array is terminated when the target is found. As more and more nontarget elements are added to the scene, it takes longer and longer to scan the array to find the target; 50 ms per item is typical (although as we have said, this time varies continuously over a large range of values).

In the other major class of models, all elements of the visual input compete in parallel for visual processing (Atkinson et al 1969, Bundesen 1990, Duncan & Humphreys 1989, Sperling 1967). This class includes the biased competition account that has been the theme of this review so far.

The difficulties of distinguishing between parallel and serial models on the basis of reaction time data are well known (Townsend 1971), particularly because recent serial models have become hybrids with both serial and parallel component processes. To explain pop-out effects with targets defined by the conjunction of several features, for example, both Guided Search (Wolfe et al 1989) and Feature Integration Theory (Treisman & Sato 1990) incorporate parallel top-down processes to identify all regions in the visual field that share target features. Another interesting hybrid is the spatial and object search model of Grossberg et al (1994), which explains both easy and difficult search on the basis of grouping and recognition operations recursively applied in parallel across the visual field.

Unfortunately, the physiological data on object search in IT cortex (Chelazzi et al 1993) described above do not allow us to distinguish conclusively between serial and parallel mechanisms. The fact that search arrays initially activate cells selective for any of the component elements, targets or nontargets, is consistent with the biased competition model in which all objects are prcessed in parallel. However, it is possible that what seems to be an initial parallel activation lasting 200 ms is actually a serial activation, with the serial scanner switching between elements at a rate too rapid to discern in the neural data. The strongest argument against the serial model is that known memory mechanisms in IT cortex are sufficient to explain the results without invoking a hidden serial process.

The time it takes to recognize one object and release processing capacity

for another, or the attentional dwell time, is a critical issue in comparing the different models. To make such a measurement, a brief temporal interval is introduced between two targets, e.g. two letters to be identified. If the time between presentation of the targets is shorter than the attentional dwell time, there should be interference, as both targets will compete for processing capacity. According to typical serial models, which posit rapid attentional scanning of objects in a scene, each object consumes processing capacity for only a few dozen milliseconds; thus, the attentional dwell time is short and interference should be eliminated with correspondingly short interstimulus intervals. Attentional dwell times can be much greater in parallel models because more than one object in a scene is processed at once (with increasing interference as the number of objects is increased). Thus, interference may last for far longer periods of time. A recent study using this method of sequential target presentation found interference lasting for several hundred milliseconds, consistent with parallel models (Duncan et al 1994; see also Pashler & Badgio 1987).

CONCLUSIONS

By way of contrast, it would be useful to consider again the standard model of selective visual attention widely accepted in neuroscience. According to this view, attention focuses on one region of the visual field at a time. It is mediated by a system of spatially mapped structures that enhance processing in visual cortex at attended locations and reduce it at unattended ones. The components of this system are revealed by neglect and extinction syndromes following lesions. Attention is unnecessary for simple feature discriminations but resolves the binding problem by linking together the output of cells coding different elemental features of the attended object. It is a serial, high-speed scanning mechanism moving from one location to the next in around 50 ms.

The data we have reviewed cast doubt over many of the postulates of the standard view. Instead, they suggest the following conclusions:

1. At several points between input and response, objects in the visual field compete for limited processing capacity and control of behavior.
2. This competition is biased in part by bottom-up neural mechanisms that separate figures from their background (in both space and time) and in part by top-down mechanisms that select objects of relevance to current behavior. Such bias can be controlled by many stimulus attributes, including selection by spatial location, by simple object features, and by complex conjunctions of features.
3. Within the ventral stream, which underlies object recognition, top-down biasing inputs resolve competition mainly between objects located within

the same receptive field. These mechanisms may work in a similar fashion for both object and spatial selection. In some cases, these inputs are directly revealed through elevation of the maintained activity of cells coding the location or feature of the expected item. The critical difference between spatial and feature selection may be the source and nature of the selection template.

4. Because many spatially mapped structures contribute to competition, unilateral lesions will often cause neglect and extinction syndromes that do not necessarily imply a specific role in attentional control.

5. The top-down selection templates for both locations and objects are probably derived from neural circuits mediating working memory, perhaps especially in prefrontal cortex.

6. Objects act as wholes in neural competition. The construction of object representations from the conjunction of many different features appears, in many cases, to occur in parallel across the visual field before individual objects are selected and, hence, prior to any attentional binding.

7. Though the matter remains controversial, according to our analysis attention is not a high-speed mental spotlight that scans each item in the visual field. Rather, attention is an emergent property of slow, competitive interactions that work in parallel across the visual field.

ACKNOWLEDGMENTS

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