

# Finding a face in the crowd: parallel and serial neural mechanisms of visual selection

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**Abstract:** At any given moment, our visual system is confronted with more information than it can process. Thus, attention is needed to select behaviorally relevant information in a visual scene for further processing. Behavioral studies of attention during visual search have led to the distinction between serial and parallel mechanisms of selection. To find a target object in a crowded scene, for example a “face in a crowd”, the visual system might turn on and off the neural representation of each object in a serial fashion, testing each representation against a template of the target object. Alternatively, it might allow the processing of all objects in parallel, but bias activity in favor of those neurons representing critical features of the target, until the target emerges from the background. Recent neurophysiological evidence shows that both serial and parallel selections take place in neurons of the ventral “object-recognition pathway” during visual search tasks in which monkeys freely scan complex displays to find a target object. Furthermore, attentional selection appears to be mediated by changes in the synchrony of responses of neuronal populations in addition to the modulation of the firing rate of individual neurons.

**Keywords:** attention; selection; saccades; visual search; serial; parallel; area V4; synchrony

## Introduction

Vision is of primary importance in gathering information about the surrounding world, and we spend much of our time engaged in visual search to find and process behaviorally relevant information in crowded scenes. When viewers know the location of the relevant object, the brain mechanisms that guide spatial attention to the object are largely overlapping with those for selecting the targets for eye movements (Nobre, 2001; Corbetta and Shulman, 2002), consistent with behavioral studies showing a strong functional link between spatial attention and eye movements (Kowler et al., 1995; Deubel and Schneider, 1996; Liversedge and

Findlay, 2000). Selection for attention or eye movements lead to an enhancement of the responses of visual cortex neurons to the relevant object, at the expense of distractors (Luck et al., 1997; Colby and Goldberg, 1999; Seidemann and Newsome, 1999; Treue and Maunsell, 1999; Andersen and Buneo, 2002), leaving object recognition mechanisms in the temporal cortex with only a single relevant stimulus at a time (Desimone and Duncan, 1995). However, in most common visual scenes, viewers rarely know the specific location of the relevant object in advance — instead, they must search for it, based on its distinguishing features such as color or shape, which is commonly termed visual search.

For decades, psychologists have debated on how the brain filters out irrelevant information and focuses attention on information that matters, with

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many debates centered around the roles of serial and parallel mechanisms in selection (Shiffrin and Schneider, 1977; Treisman and Gelade, 1980; Nakayama and Silverman, 1986; Wolfe et al., 1989; Townsend, 1990). This distinction can be illustrated by considering a complex visual search such as finding Waldo in a crowded page of a “Where’s Waldo?” book. When searching for Waldo, one possibility is that the brain scans the page spatially (serial processing) like a mental spotlight (Posner et al., 1980) moving across an otherwise dark page. In this model, the attentional spotlight would track across the page, checking each object within its “field of illumination” against a mental image of Waldo. Another possibility is that the brain takes in the entire page at once and gradually zooms in on relevant features such as color and shape (parallel processing). In this model, based for example on a bias towards Waldo’s red-striped shirt, objects with the color red would gradually stand out from the cluttered background. Here, we review recent studies from our lab, as well as others, that have investigated the brain mechanisms underlying top-down, feature-based selection during visual search guided by the knowledge of the target’s visual properties.

### Parallel selection during visual search

The key element of parallel search models is a neural bias in favor of stimuli containing features (e.g., color or shape) of the searched-for target that occurs throughout the visual field and throughout the time period of the search, long before a target is identified. We recently investigated the presence of such a bias in the activity of visual cortical neurons in monkeys that freely scanned complex visual search arrays to find a target defined by color (Fig. 1A), shape, or both (Fig. 1B) (Bichot et al., 2005). Recordings were conducted in area V4, a key area of the ventral stream for object recognition (Mishkin et al., 1983), where neurons have smaller receptive fields (RFs) compared with the extremely large RFs in inferior temporal (IT) cortex and are selective for basic stimulus features such as color, orientation, and simple shapes (Desimone et al., 1985; Desimone and Schein,

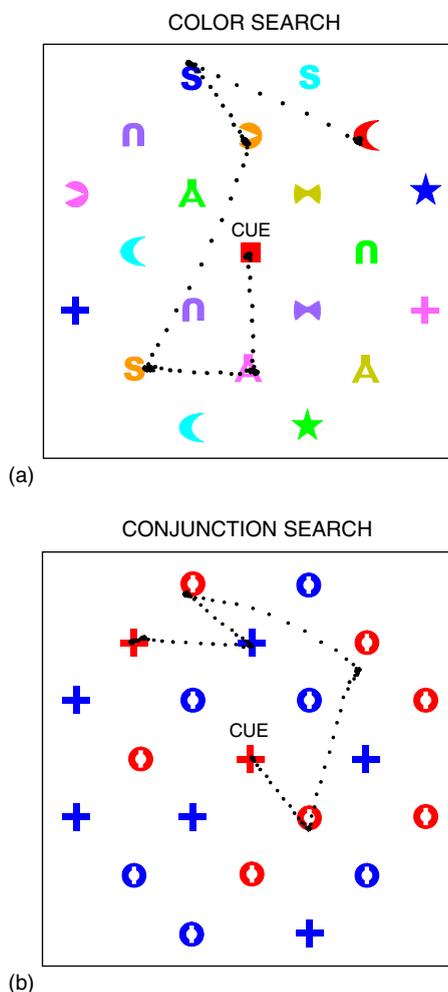


Fig. 1. Free-viewing visual search tasks. (a) Examples of a color search trial and a (b) conjunction search trial. The black dots show the eye position of the monkey during representative correctly performed trials. In all searches, monkeys fixated a central fixation spot that was then replaced by a central cue. The cues at the center of the screen are shown for illustration purposes only as they were extinguished before the onset of the search array in the experiment. During color search, the cue was a colored square that instructed monkeys with the color of the target, and during shape search, the cue was a gray shape that instructed monkeys with the shape of the target. When color was relevant, shape was irrelevant, and vice versa. During conjunction search, the cue (and target) was one combination of two colors and two shapes, and the distractors either shared the color, shape or no feature with the target. Monkeys were trained to find and fixate the target stimulus for a prescribed duration to receive reward. As shown in the examples, monkeys made several saccades (~5.8 per trial across all search types) before finding the target.

1987; Schein and Desimone, 1990). Furthermore, previous studies have shown that attentional modulation in area V4 is larger than in areas V1 and V2 and therefore easier to study (Luck et al., 1997).

To test for parallel, feature-based biasing, Bichot et al. (2005) specifically considered responses to stimuli in the RF of neurons at times when the monkey was actively “attending” elsewhere, when the monkey was preparing to make a saccade to a stimulus outside the RF. More specifically, the response to an unselected RF stimulus with the neuron’s preferred or nonpreferred color was compared on trials during which the cue was of the preferred or nonpreferred color for the neuron (Fig. 2A). When a stimulus of the preferred color was in the RF, neurons gave enhanced responses when it matched the cue color. Responses to a RF stimulus of the nonpreferred color, on the other hand, were not modulated by cue color. Similar results were found during shape search taking into account the neurons’ selectivity for stimulus shapes. Thus, neurons responded most strongly when an unselected RF stimulus with the preferred feature was the search target, even though the stimulus was not selected for a saccadic eye movement. For example, if the animal was searching for red, the cells preferred red, and there happened to be a red stimulus inside the RF; this is when firing rate was enhanced, even though the animal was preparing an eye movement to a different stimulus. Furthermore, when the cue was of the preferred color of the neurons, responses to stimuli with colors similar to the cue color also showed some enhancement, explaining why the animals tended to fixate distractors similar to the target.

The feature-based bias observed by Bichot et al. (2005) is consistent with the findings of another study examining neural activity in area V4 during free-viewing visual search (Mazer and Gallant, 2003). In that study, monkeys were trained to search for a target grayscale natural image patch among distractor ones. Across all fixations, they found significant differences in the activity of about one in four V4 neurons across the different search targets. However, it is not clear whether the overall enhancement of neural responses in that study for a particular search target affected all stimuli regardless of features and their similarity to

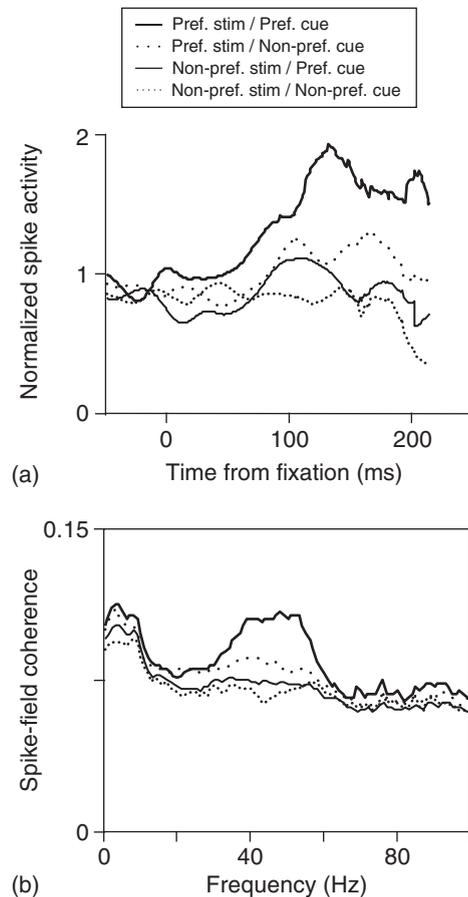


Fig. 2. Feature-related enhancement of neuronal activity and spike-field synchronization in area V4 during color search. (a) Normalized firing rates averaged over a population of V4 neurons during color search trials during fixations at the end of which the monkey made a saccade away from the RF. Thick lines show responses when the stimulus in the RF was of the preferred color for the recorded neurons; thin lines show responses when the stimulus was of the nonpreferred color; solid lines show responses on trials in which the cue was the preferred color; and dotted lines show responses on trials in which the cue was the nonpreferred color. (b) Spike field coherence for the same conditions.

the target, and whether the results were confounded by differences in gaze patterns with different search targets.

As with most studies of the neural substrates of attention (Desimone and Duncan, 1995; Maunsell, 1995), the findings described above show a bias for stimuli that are likely to be the search targets resulting from the increase in the firing rate of

individual neurons in response to those stimuli. However, another potential “amplifier” of the effects of one population of neurons on another is the synchronization of activity in the input population (Gray et al., 1989; Salinas and Sejnowski, 2000; Kara and Reid, 2003). Small changes in high frequency synchronization of spike trains with attention at one stage might lead to pronounced firing rate changes at subsequent stages (Niebur et al., 1993; Salinas and Sejnowski, 2000) because cells generally have short synaptic integration times. Indeed, V4 neurons synchronize their activity when attention is directed to their RFs (Fries et al., 2001), as do neurons in parietal cortex during a memory-saccade task (Pesaran et al., 2002). Also, in monkey somatosensory cortex, it has been reported that cells synchronize their activity when monkeys perform a tactile task compared to a visual task, presumably due to an increase in “tactile attention” in that task (Steinmetz et al., 2000).

To investigate potential changes in neuronal synchronization with feature-based attention, Bichot et al. (2005) measured the coherence between spikes and the local field potential (LFP) (Fries et al., 1997; Jarvis and Mitra, 2001). Spike-field coherence measures phase synchronization between the LFP and spike times as a function of frequency, and is independent of any changes in the firing rate of the spikes and in the power spectrum of the LFP. Coherence for a given frequency ranges from 0 (when the spikes do not have any systematic phase relation to the LFP component at this frequency) to 1 (when all spikes appear at exactly the same phase relation relative to this frequency component). During color search, similar to the effects found on firing rates, neurons increased their synchronization in the gamma-range (30–60 Hz) when an unselected RF stimulus with the preferred color was the target that the animal was searching for (Fig. 2B). There was also a smaller increase in gamma-band synchrony when the preferred color was cued and distractors with similar colors fell in the RF along with a marginal increase for distractors with the nonpreferred color. Similar effects on synchrony were found during shape search. Thus, these results suggest that when the animal is searching for a particular feature, the neurons that prefer that feature begin

to synchronize their activity, reaching maximal synchronization when a stimulus with that feature falls within their RF (e.g., when the animal is searching for red, the neurons prefer red, and a red stimulus falls within the RF).

The results described so far show that neurons gave enhanced responses and synchronized their activity in the gamma-range whenever a preferred stimulus in their RF was the target the animal was looking for, but had not found as yet. However, it is not clear from these results whether a distractor with a target feature would share in the bias for target features as proposed by parallel models of visual search (Cave and Wolfe, 1990; Desimone and Duncan, 1995). For example, when searching for a red cross among red circles, green crosses, and green circles, we should see evidence for enhancement of responses and/or synchrony when the RF stimulus contains a single feature of the target (i.e., red circle or green cross) but is not, itself, a target as it lacks the other target feature. Indeed, we found that during a conjunction search, neurons increased and synchronized their activity for unselected distractors in the RF with the preferred color when that color was shared with the target (Fig. 3). Interestingly, although sharing in the bias for the target shape also led to neural enhancement, the magnitude of the effect was much smaller, consistent with behavioral evidence that the monkey used the color information more than the shape information in guiding its search to the color–shape conjunction target (i.e., fixated distractors with the target color more often than distractors with the target shape). Altogether, these results suggest that responses are enhanced whenever a RF stimulus contains a preferred feature of the neurons, and that feature is used in guiding the search for the target.

The source of the top-down bias on V4 activity most likely originates, at least in part, in prefrontal cortex, which has been shown to play an important role in working memory and executive control (Miller and Cohen, 2001). Accordingly, during a match-to-sample task, sample-selective delay activity in prefrontal cortex is maintained throughout the trial even when other test stimuli intervene during the delay, whereas delay activity in IT cortex is disrupted by intervening stimuli (Miller

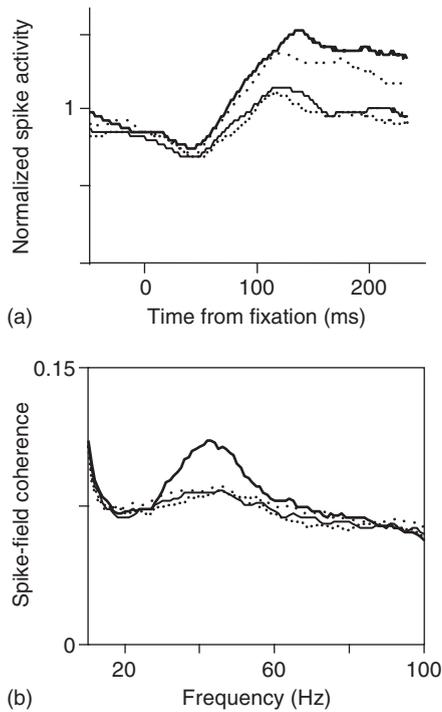


Fig. 3. Color-related enhancement of neuronal activity and spike-field synchronization in area V4 during conjunction search. Conventions are as in Fig. 2.

et al., 1996). Consistent with the idea that feedback inputs from prefrontal cortex to visual cortex bias activity in favor of behaviorally relevant stimuli, recent preliminary evidence shows that prefrontal lesions impair monkeys' ability to attend to stimuli based on color cues, but not to stimuli that are salient and pop-out (Rossi et al., 2001).

### Serial selection during visual search

Although both the behavioral and the neural evidence for parallel processing during the visual search tasks described above is compelling, it is equally clear that these searches have a serial component in that the monkeys make several saccades to find the target (Fig. 1). To test for spatial attention effects on responses, Bichot et al. (2005) compared neural responses to any stimulus in the RF when it was either selected for a saccade or the saccade was made to a stimulus outside the RF during color and shape feature searches. Neurons

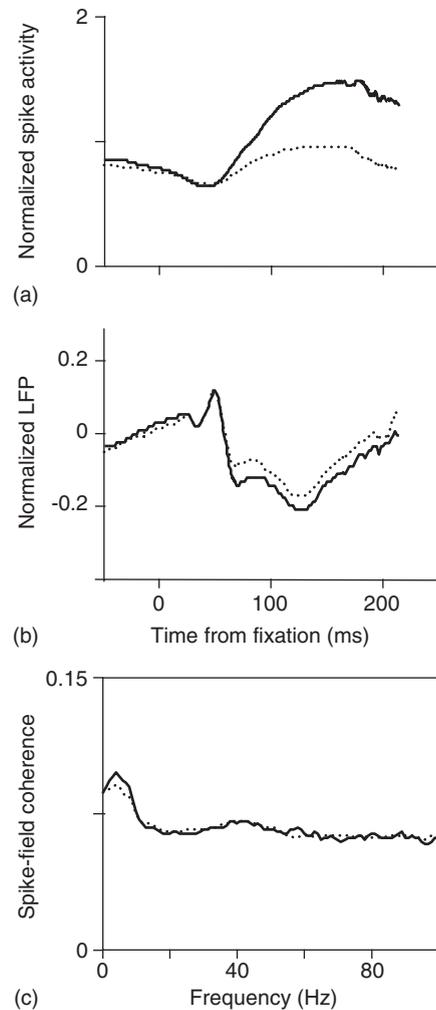


Fig. 4. Saccadic enhancement in area V4 during feature searches. (a) Normalized firing rates for the population of neurons when a saccade was made to a stimulus inside the RF (solid line) and when a saccade was made to a stimulus outside the RF (dotted line) across all saccades. Data from color and shape searches were combined. (b) and (c) Average normalized LFP and spike-field coherence for the same conditions.

responded more strongly to a stimulus in the RF when it was the goal of the impending saccade (Fig. 4A), consistent with the findings of Mazer and Gallant (2003), using a similar free-viewing visual search task. Furthermore, both the magnitude (Fig. 4B) and the spectral power of the LFP in the gamma-frequency range were significantly modulated by monkeys' decision to make a saccade to the RF stimulus. However, despite such

strong modulation of neuronal firing rates and LFPs, spike-field coherence was unaffected by spatial selection (Fig. 4C).

The lack of modulation of neuronal synchrony with spatial selection during visual search stands in contrast to changes in synchrony that were observed with feature selection in the same search. Furthermore, superficially at least, this result seems at odds with a previous finding by Fries et al. (2001) that gamma-frequency synchronization increases and beta-frequency synchronization decreases when a monkey attends to a stimulus inside the RF of neurons (Fig. 5). A critical factor appears to be the length of time for which attention is maintained for a given feature or location. In the Fries et al. study, monkeys monitored and attended to the target location for up to several seconds, whereas during visual search the time that the animal takes to attend to the location of the next stimulus that will be the target of a saccade is only about 250 ms. The effect of feature-based attention on synchrony during visual search is consistent with this explanation as the animal maintains a state of attention to stimulus features

lasting several seconds. Thus, it seems plausible that attentional effects on synchrony take longer to develop than attentional effects on firing rate.

The modulation of responses by the locus of spatial attention that we (Bichot et al., 2005) and others (Mazer and Gallant, 2003) have found in V4 likely involve feedback from structures involved in spatial attention and saccade production. One such structure, the frontal eye field (FEF), is reciprocally connected with areas of both the dorsal and the ventral visual processing streams, and these connections are topographically organized (Schall et al., 1995). Consistent with the idea that feedback from FEF to visual cortex plays a role in spatial selection, recent studies by Moore and colleagues have shown that subthreshold stimulation of FEF improves perceptual ability (Moore and Fallah, 2004) and enhances the visual responses of V4 neurons (Moore and Armstrong, 2003), similar to the effects of spatial attention on perception and neuronal responses.

Studies of neural selection in FEF during visual search have led to the proposal that this area represents the behavioral significance of stimuli

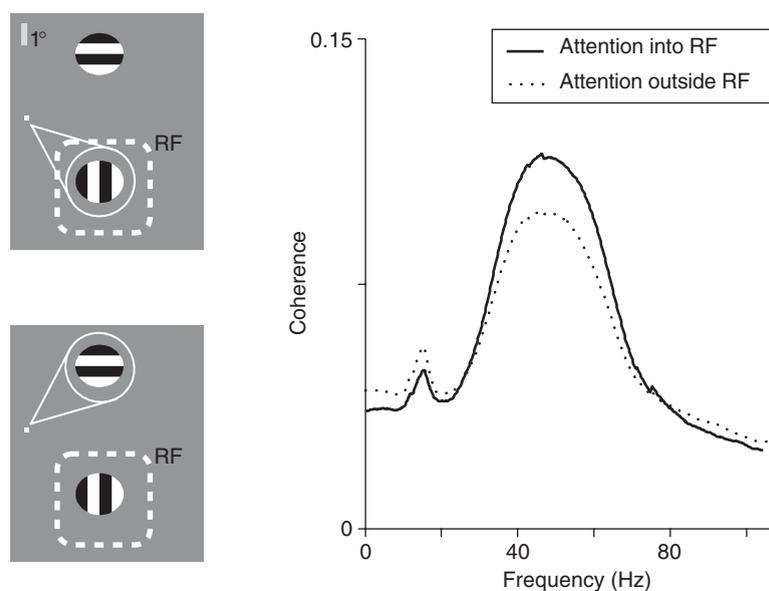


Fig. 5. Enhancement of spike-field synchronization by spatial attention in area V4. Spike-field coherence is plotted when the monkey attended to a drifting grating inside the RF (solid line) and when the monkey attended to one outside the RF (dotted line). Both gratings were presented on each trial, and the monkey was instructed to attend to one of them in blocks of trials. In the task displays, the RF is illustrated by the dotted square, and the location of attention is illustrated by the cone.

regardless of their visual features (Thompson and Bichot, 2005), much like the concept of a “saliency map” found in many models of visual search (Koch and Ullman, 1985; Treisman, 1988; Cave and Wolfe, 1990; Olshausen et al., 1993; Itti and Koch, 2001). During conjunction search for example, visually responsive FEF neurons initially respond indiscriminately to the target and distractors of the search array (Bichot and Schall, 1999), consistent with the fact that FEF neurons are not selective for visual features such as color (Mohler et al., 1973). However, over time, these neurons not only discriminate the target from distractors, but also discriminate among distractors on the basis of their similarity to the target, even though a saccade is only made to the target location (Fig. 6). In other words, while the highest activation was observed when the target was in the neurons’ RF, the activity in response to RF distractors that shared the target color or shape was also relatively enhanced. Such a spatial map of potential targets would result from topographically organized, convergent input from visually selective neurons with activity biased for target features, and in turn, spatial selection within this map would modulate the activity of visual neurons through feedback connections enhancing the representation of a stimulus selected for an eye movement (Hamker, 2005). Other structures that likely encode a map of behavioral relevance for spatial selection include the lateral intraparietal area (Gottlieb et al., 1998) and the superior colliculus (Findlay and Walker, 1999; McPeck and Keller, 2002).

## Conclusion

We have reviewed recent neurophysiological studies showing that both serial and parallel processing of visual information takes place in the brain during visual search, consistent with hybrid models of visual selection (Cave and Wolfe, 1990; Hamker, 2005). Furthermore, these processes are observed in the same brain area and in the same neurons (e.g., area V4) (Mazer and Gallant, 2003; Bichot et al., 2005).

The search for a target based on its features appears to enhance and synchronize the activity of populations of V4 neurons that are selective for and

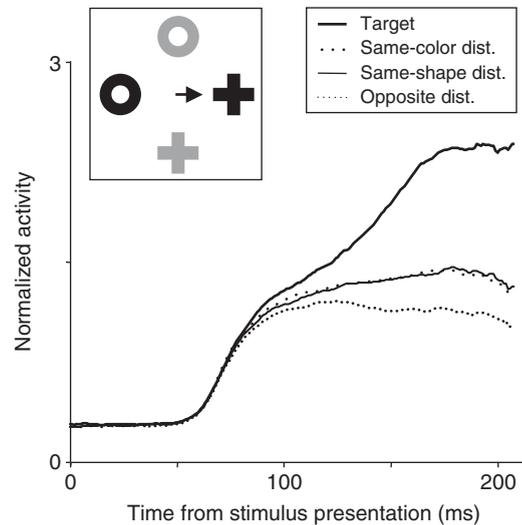


Fig. 6. Visual selection in FEF during conjunction search. Normalized firing rates averaged over a population of visually responsive FEF neurons on correctly performed trials (i.e., first and only saccade was made to the target illustrated by the arrow in the example display). Activity aligned on the time of search array presentation is shown when the target was in the RF (thick solid line); when a distractor that shared the target color (i.e., same-color distractor) was in the RF (thick dotted); when a distractor that shared the target shape (i.e., same-shape distractor) was in the RF (thin solid); and when a distractor that did not share any features with the target (i.e., opposite distractor) was in the RF (thin dotted). In the example search display, stimuli of one color are shown in black and stimuli of the other color are shown in gray.

respond preferentially to those features. As a result, stimuli that are similar to the target or that share target features are better represented in the cortex, leading to serial selection among candidate stimuli (Fig. 7). These results offer an explanation for why some visual search tasks are difficult, including some, where targets are defined by the conjunction of different features. Of course, if the results of parallel processing were as clean as depicted in Fig. 7, and the target selection mechanism picked the stimulus location with the highest activation (i.e., winner-take-all), finding the search target would require only one attentional shift or saccadic eye movement. However, evidence from the reviewed studies clearly shows a serial component to the visual search in that several stimuli are fixated before the target is found. Several sources of variability in the activation map from which a target is selected

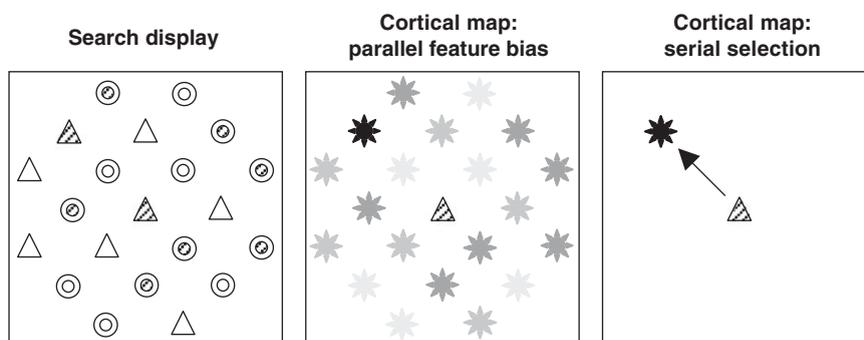


Fig. 7. Schematic illustration of selection mechanisms during a conjunction search task. Left: example stimulus display. Stimuli of one color are shown as filled with diagonal lines, and the ones of the other color are shown as not filled. Middle: representation of stimulus display in the cortex with a bias in favor of potential targets, illustrated by the intensity of the stimulus representation, as a result of parallel, feature-related selection throughout the visual field. Right: the bias for potential targets triggers spatial selection mechanisms resulting in eye movements (illustrated by the arrow towards the target location).

would account for the inability of the visuomotor system to detect the target immediately. For example, the guided-search model of visual selection has attributed this variability to simple “noisiness” in the firing rates of neurons (Cave and Wolfe, 1990), consistent with the known variability of neuronal responses (Henry et al., 1973; Tolhurst et al., 1983; Shadlen et al., 1996; Bichot et al., 2001). The feature-gate model of selection, on the other hand, suggests the possibility that bottom-up interactions between stimuli are a source of variability in their neural representation (Cave et al., 2005). Furthermore, decreased acuity for peripheral stimuli and cortical magnification also affect the neural representation of stimuli, and it has been shown that high probability detection of targets occurs only within a restricted area surrounding the fixation point (Motter and Belky, 1998).

Finally, several studies have shown that neuronal synchrony (especially in the gamma-frequency range) plays an important role in spatial selection (Fries et al., 2001; Pesaran et al., 2002) as well as featural selection (Bichot et al., 2005), suggesting that synchronizing signals could be a general way the brain focuses on important information. Gamma-frequency synchronization may also contribute to the increased “activation” found in functional magnetic resonance imaging (fMRI) studies of attention, based on findings from a recent study suggesting that the BOLD signal measured in fMRI is closely correlated with synchronous

activity in the gamma-range (Kayser et al., 2004). Furthermore, the contribution of neural synchrony to feature-based selection during visual search (Bichot et al., 2005) lends additional support to the idea that synchronized activity has an amplifying role in relaying certain types of behaviorally relevant information from one neural population to the next. Although it has been argued that gamma-frequency synchronization solves the binding problem in visual perception (Engel et al., 1997), the results described here suggest that synchrony may play a much broader role in neural processing.

## References

- Andersen, R.A. and Buneo, C.A. (2002) Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.*, 25: 189–220.
- Bichot, N.P., Rossi, A.F. and Desimone, R. (2005) Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, 308: 529–534.
- Bichot, N.P. and Schall, J.D. (1999) Effects of similarity and history on neural mechanisms of visual selection. *Nat. Neurosci.*, 2: 549–554.
- Bichot, N.P., Thompson, K.G., Chenthal Rao, S. and Schall, J.D. (2001) Reliability of macaque frontal eye field neurons signaling saccade targets during visual search. *J. Neurosci.*, 21: 713–725.
- Cave, K.R., Kim, M.S., Bichot, N.P. and Sobel, K.V. (2005) The FeatureGate model of visual selection. In: Itti, L., Rees, G. and Tsotsos, J.K. (Eds.), *Neurobiology of Attention*. Elsevier Academic Press, San Diego, CA, pp. 547–552.
- Cave, K.R. and Wolfe, J.M. (1990) Modeling the role of parallel processing in visual search. *Cogn. Psychol.*, 22: 225–271.

- Colby, C.L. and Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.*, 22: 319–349.
- Corbetta, M. and Shulman, G.L. (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.*, 3: 201–215.
- Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.*, 18: 193–222.
- Desimone, R. and Schein, S.J. (1987) Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *J. Neurophysiol.*, 57: 835–868.
- Desimone, R., Schein, S.J., Moran, J. and Ungerleider, L.G. (1985) Contour, color and shape analysis beyond the striate cortex. *Vision Res.*, 25: 441–452.
- Deubel, H. and Schneider, W.X. (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res.*, 36: 1827–1837.
- Engel, A.K., Roelfsema, P.R., Fries, P., Brecht, M. and Singer, W. (1997) Role of the temporal domain for response selection and perceptual binding. *Cereb. Cortex*, 7: 571–582.
- Findlay, J.M. and Walker, R. (1999) A model of saccade generation based on parallel processing and competitive inhibition. *Behav. Brain Sci.*, 22: 661–674., discussion 674–721.
- Fries, P., Reynolds, J.H., Rorie, A.E. and Desimone, R. (2001) Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*, 291: 1560–1563.
- Fries, P., Roelfsema, P.R., Engel, A.K., Konig, P. and Singer, W. (1997) Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proc. Natl. Acad. Sci. USA*, 94: 12699–12704.
- Gottlieb, J.P., Kusunoki, M. and Goldberg, M.E. (1998) The representation of visual salience in monkey parietal cortex. *Nature*, 391: 481–484.
- Gray, C.M., Konig, P., Engel, A.K. and Singer, W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, 338: 334–337.
- Hamker, F.H. (2005) The reentry hypothesis: the putative interaction of the frontal eye field, ventrolateral prefrontal cortex, and areas V4, IT for attention and eye movement. *Cereb. Cortex*, 15: 431–447.
- Henry, G.H., Bishop, P.O., Tupper, R.M. and Dreher, B. (1973) Orientation specificity and response variability of cells in the striate cortex. *Vision Res.*, 13: 1771–1779.
- Itti, L. and Koch, C. (2001) Computational modelling of visual attention. *Nat. Rev. Neurosci.*, 2: 194–203.
- Jarvis, M.R. and Mitra, P.P. (2001) Sampling properties of the spectrum and coherency of sequences of action potentials. *Neural Comput.*, 13: 717–749.
- Kara, P. and Reid, R.C. (2003) Efficacy of retinal spikes in driving cortical responses. *J. Neurosci.*, 23: 8547–8557.
- Kayser, C., Kim, M., Ugurbil, K., Kim, D.S. and Konig, P. (2004) A comparison of hemodynamic and neural responses in cat visual cortex using complex stimuli. *Cereb. Cortex*, 14: 881–891.
- Koch, C. and Ullman, S. (1985) Shifts in selective visual attention: towards the underlying neural circuitry. *Hum. Neurobiol.*, 4: 219–227.
- Kowler, E., Anderson, E., Doshier, B. and Blaser, E. (1995) The role of attention in the programming of saccades. *Vision Res.*, 35: 1897–1916.
- Liversedge, S.P. and Findlay, J.M. (2000) Saccadic eye movements and cognition. *Trends Cogn. Sci.*, 4: 6–14.
- Luck, S.J., Chelazzi, L., Hillyard, S.A. and Desimone, R. (1997) Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.*, 77: 24–42.
- Maunsell, J.H. (1995) The brain's visual world: representation of visual targets in cerebral cortex. *Science*, 270: 764–769.
- Mazer, J.A. and Gallant, J.L. (2003) Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map. *Neuron*, 40: 1241–1250.
- McPeck, R.M. and Keller, E.L. (2002) Saccade target selection in the superior colliculus during a visual search task. *J. Neurophysiol.*, 88: 2019–2034.
- Miller, E.K. and Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.*, 24: 167–202.
- Miller, E.K., Erickson, C.A. and Desimone, R. (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.*, 16: 5154–5167.
- Mishkin, M., Ungerleider, L.G. and Macko, K.A. (1983) Object vision and spatial vision: two cortical pathways. *Trends Neurosci.*, 6: 414–417.
- Mohler, C.W., Goldberg, M.E. and Wurtz, R.H. (1973) Visual receptive fields of frontal eye field neurons. *Brain Res.*, 61: 385–389.
- Moore, T. and Armstrong, K.M. (2003) Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, 421: 370–373.
- Moore, T. and Fallah, M. (2004) Microstimulation of the frontal eye field and its effects on covert spatial attention. *J. Neurophysiol.*, 91: 152–162.
- Motter, B.C. and Belky, E.J. (1998) The zone of focal attention during active visual search. *Vision Res.*, 38: 1007–1022.
- Nakayama, K. and Silverman, G.H. (1986) Serial and parallel processing of visual feature conjunctions. *Nature*, 320: 264–265.
- Niebur, E., Koch, C. and Rosin, C. (1993) An oscillation-based model for the neuronal basis of attention. *Vision Res.*, 33: 2789–2802.
- Nobre, A.C. (2001) The attentive homunculus: now you see it, now you don't. *Neurosci. Biobehav. Rev.*, 25: 477–496.
- Olshausen, B.A., Anderson, C.H. and Van Essen, D.C. (1993) A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *J. Neurosci.*, 13: 4700–4719.
- Pesaran, B., Pezaris, J.S., Sahani, M., Mitra, P.P. and Andersen, R.A. (2002) Temporal structure in neuronal activity during working memory in macaque parietal cortex. *Nat. Neurosci.*, 5: 805–811.
- Posner, M.I., Snyder, C.R. and Davidson, B.J. (1980) Attention and the detection of signals. *J. Exp. Psychol.*, 109: 160–174.
- Rossi, A.F., Bichot, N.P., Desimone, R. and Ungerleider, L.G. (2001) Top-down, but not bottom-up: deficits in target selection in monkeys with prefrontal lesions. *J. Vis.*, 1: 18a.
- Salinas, E. and Sejnowski, T.J. (2000) Impact of correlated synaptic input on output firing rate and variability in simple neuronal models. *J. Neurosci.*, 20: 6193–6209.

- Schall, J.D., Morel, A., King, D.J. and Bullier, J. (1995) Topography of visual cortex connections with frontal eye field in macaque: convergence and segregation of processing streams. *J. Neurosci.*, 15: 4464–4487.
- Schein, S.J. and Desimone, R. (1990) Spectral properties of V4 neurons in the macaque. *J. Neurosci.*, 10: 3369–3389.
- Seidemann, E. and Newsome, W.T. (1999) Effect of spatial attention on the responses of area MT neurons. *J. Neurophysiol.*, 81: 1783–1794.
- Shadlen, M.N., Britten, K.H., Newsome, W.T. and Movshon, J.A. (1996) A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *J. Neurosci.*, 16: 1486–1510.
- Shiffrin, R.M. and Schneider, W. (1977) Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychol. Rev.*, 84: 127–190.
- Steinmetz, P.N., Roy, A., Fitzgerald, P.J., Hsiao, S.S., Johnson, K.O. and Niebur, E. (2000) Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature*, 404: 187–190.
- Thompson, K.G. and Bichot, N.P. (2005) A visual salience map in the primate frontal eye field. *Prog. Brain Res.*, 147: 251–262.
- Tolhurst, D.J., Movshon, J.A. and Dean, A.F. (1983) The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vision Res.*, 23: 775–785.
- Townsend, J.T. (1990) Serial vs. parallel processing: sometimes they look like tweedledum and tweedledee but they can (and should) be distinguished. *Psychol. Sci.*, 1: 46–54.
- Treisman, A. (1988) Features and objects: the fourteenth Bartlett memorial lecture. *Q. J. Exp. Psychol. A*, 40: 201–237.
- Treisman, A.M. and Gelade, G. (1980) A feature-integration theory of attention. *Cogn. Psychol.*, 12: 97–136.
- Treue, S. and Maunsell, J.H. (1999) Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *J. Neurosci.*, 19: 7591–7602.
- Wolfe, J.M., Cave, K.R. and Franzel, S.L. (1989) Guided search: an alternative to the feature integration model for visual search. *J. Exp. Psychol. Hum. Percept. Perform.*, 15: 419–433.