The cognitive neuroscience of visual attention

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In current conceptualizations of visual attention, selection takes place through integrated competition between recurrently connected visual processing networks. Selection, which facilitates the emergence of a 'winner' from among many potential targets, can be associated with particular spatial locations or object properties, and it can be modulated by both stimulus-driven and goal-driven factors. Recent neurobiological data support this account, revealing the activation of striate and extrastriate brain regions during conditions of competition. In addition, parietal and temporal cortices play a role in selection, biasing the ultimate outcome of the competition.

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Abbreviations
ERP event-related potential
fMRI functional magnetic resonance imaging
MEG magnetoencephalography
MST medial superior temporal
MT middle temporal
PET positron emission tomography
SOA stimulus onset asynchrony
TMS transcranial magnetic stimulation
TEO temporal occipital
WTA winner-take-all

Introduction

The term 'selective attention' generally refers to the set of operations that determine which of several possible inputs will be analyzed past the level at which all may be processed in parallel. Standard conceptualizations of selective attention have undergone numerous transformations in the four decades following Broadbent's [1] initial proposal. Early theories drew analogies between selection and a filtering mechanism that operated in accordance with a set of either early perceptual [1] or later semantic [2] criteria. Later theories recast attention as the selective distribution of a limited supply of cognitive resources (see e.g. [3]); this shifted the perceived role of attention from a discrete gateway separating different levels of processing to that of a modulatory influence that could increase or decrease the efficiency of demanding processing tasks. Considered in this way, attention was a far more flexible mechanism, capable of facilitating or inhibiting processing of the input. Moreover, this perspective afforded an analysis of selection phenomena in terms of costs and benefits (see e.g. [4,5]): for example, an increase in the efficiency of processing a selected portion of input necessitated a con-

comitant decrease in processing other, nonselected portions of input.

A state of competition between different possible inputs supplanted the need for a discrete filtering process. In simple competition models, the input receiving the greatest proportion of resources (e.g. as a result of more salient bottom-up attributes) would be most completely analyzed, and the contents of this analysis would be communicated to further stages of processing. A specialized attentional mechanism that could alter the distribution of these resources could, in essence, facilitate the processing of the information in a portion of input by providing it with additional support and biasing competition in its favour. How such a mechanism might identify a discrete portion of input for preferential processing continues to be the source of considerable debate, as some studies implicated a mechanism that selected input associated with a specific set of spatial locations (see e.g. [4]), whereas others pointed to a mechanism that selected input associated with a representation of an object that had already been fully parsed in accordance with pre-attentive Gestalt principles (see e.g. [6]). Most importantly, it was unclear how competition and modulation might be related to processing in the brain.

Computational modelling, however, has provided a means of addressing these issues. Biased competition can be readily understood in terms of interactions between units in 'winner-take-all' (WTA) neural networks, and a number of neurally inspired computational models of selective attention have employed WTA network dynamics [7–9]. Moreover, recent proposals (e.g. [10,11]) have interpreted the functioning of the attentional components associated with posterior and anterior neuroanatomical regions [12] in terms of WTA interactions among lower-level representations in early visual cortical and subcortical areas, higher-level representations in the dorsal and ventral visual processing streams, and the frontal lobes (see Figure 1). According to these models, representations within the same processing region that correspond to different portions of input are mutually inhibitory, whereas those in different processing systems that correspond to the same portion of input are mutually excitatory. Thus, selection emerges from local competition and nonlocal cooperation in multiple levels of processing throughout the entire set of interconnected networks.

Competition in lower-level posterior regions will tend to be influenced by exogenous factors such as attribute salience. This will, in turn, affect competition in the higher-level, more anterior regions to which they provide input. However, endogenous factors such as task relevance or goal-driven strategies will tend to bias competition in the more intention-related anterior representations that can, in

turn, provide top-down support to posterior regions and thereby modulate the influence of exogenous factors at a lower level. This view of integrated competition between recurrently connected visual processing networks has been applied to a number of different issues in the visual attention literature (see e.g. [13–15]) and continues to gain support with the accumulation of new and converging evidence from the different methodologies encompassed by cognitive neuroscience.

Our goal in this review is to describe several examples from the body of recent work that has uncovered new characteristics of the operation of integrated competition within neuroanatomical attention networks. Although there have been many advances in our understanding of the cognitive mechanisms mediating visual selection in the past year [16,17], we will restrict our review to research that incorporates both behavioral and brain mechanisms.

Biased competition as a mechanism of selection

Recent support for the biased competition model of visual attention has been provided by both functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies. In these studies, enhancement of cortical activation or attention-related waveforms is observed under various conditions of competition: for example, when subjects perform more difficult discriminations, when distractors compete with targets and when task demands increase (e.g. when subjects have to saccade to a feature target rather than simply signalling its presence with a key press) [18••]. Moreover, when task demands increase, less activation is observed in areas associated with an irrelevant task being performed simultaneously, reflecting the decrease in processing of nonselected information [19•]. Competitive effects are also observed when, for example, stimuli are presented simultaneously rather than sequentially. In the former condition, greater activation is seen in areas V1, V2, V4, and TEO, probably reflecting the mutual suppression induced by competing stimuli [20••]; this difference in activation increases with distance from V1, possibly reflecting increased receptive field size and greater competition between neurons encoding different objects located within overlapping regions of space. Interestingly, the competition between the stimuli can be altered by focused attention: when the stimuli appear simultaneously, the suppressive interaction can be cancelled by having subjects attend selectively to one of the possible stimulus locations [20••].

Competition is also evident when attending selectively to one of two perceptual features of a stimulus, compared with dividing attention across both. For example, compared with a fixation condition, attending to the colour or shape of a stimulus manifests as increased activation in occipital and inferior temporal regions [21•]. Switching attention between the two features of a stimulus, perhaps reflecting the dynamics of the WTA, engages additional

Figure 1

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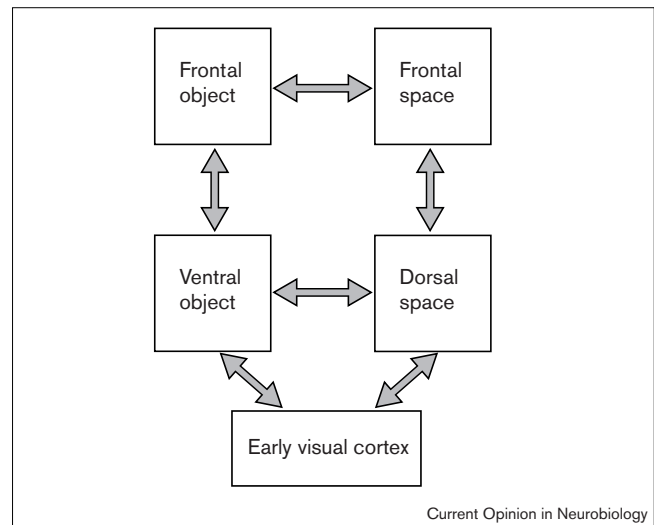
Reciprocal connections between components of the integrated competition system responsible for attentional modulation.

cortical regions and results in activation in parietal regions as well as in the cerebellum. Similar effects are observed when subjects attend selectively to the local or global level of a stimulus; this produces an amplitude modulation or increase in the early P1 components of the ERP waveform, in a region corresponding to the fusiform gyrus on PET (positron emission tomography) scans [22•]. When attention is divided between local and global levels, later, more hemisphere-specific effects are observed. Interestingly, even when subjects attend to a single dimension such as colour (e.g. to a red or to a blue stimulus), early waveforms associated with attending to one of the two colours may be localized to occipital and temporal regions, whereas later waveforms may be localized to more anterior fusiform regions and to prefrontal cortex.

Attention-related impairments resulting from damage to parietal cortex can also be interpreted as reflecting competition between targets. When letters are presented to the left and right sides of a patient with a right parietal lesion, report of the left item ('extinction') is poor at short SOAs (stimulus onset asynchrony) irrespective of whether the left or right item is presented first [23••]. Report of the contralateral item improves, however, with increasing temporal lag between the two presentations, suggesting that when the less powerful contralateral item obtains a temporal advantage, it is sufficiently activated to compete with and surpass the ipsilateral representation. Bottom-up properties of the stimulus can also affect the competition, as the contralateral item is reported more often when it shares orientation with the ipsilateral item and is, therefore, more resistant to extinction [24]. Furthermore, the competition can span more than a single modality; when a visual stimulus is presented on the ipsilateral side, it can inhibit detection of a tactile stimulus presented contralaterally [25•].

Selection by spatial location

An efficient means of selecting input is on the basis of spatial location. When spatial regions are selected covertly (i.e. in the absence of an eye movement) by pre-cueing spatial locations in which targets will probably appear, neural regions, including the right anterior cingulate gyrus and right posterior parietal cortex (intraparietal sulcus), are activated [26]. Attentional modulation occurs irrespective of whether the cues are nonsymbolic and appear peripherally [26] or are symbolic and presented centrally [27]. As would be predicted by a competition account, dividing attention between right and left locations results in longer reaction times to detect the target compared with when attention is biased to one side. An early ERP P1 component over the lateral occipital scalp accompanies the attentional benefit and a late positive deflection reveals both the attentional costs and benefits [28•]. Moreover, an event-related optical signal can be elicited in early visual areas when stimuli appear at attended, relative to unattended, locations. Whether or not the neural mechanisms associated with covert attentional shifts are identical to mechanisms dedicated to saccadic shifts remains a matter of debate. A direct comparison between a saccadic and a covert attentional shift task resulted in identical regions of activation for both, albeit to a greater extent in the eye movement task [29•]. Data from neuropsychological subjects reveal a dissociation, however, between mechanisms subserving attentional and gaze orienting [30•]: neglect patients with frontoparietal lesions make leftward eye movements without corresponding attentional shifts, whereas neglect patients with parietal lesions, who do not respond to left-sided stimuli, show different patterns of covert and overt responses to right-sided targets of differing eccentricities.

Modulation of competition: bottom-up and top-down biases

Competition between input stimuli may be modulated through biasing feedback from higher-level representations of spatial location and object structure. In addition to early striate and extrastriate areas, posterior parietal regions are activated when subjects perform difficult discriminations such as visual search for a target defined by a conjunction of multiple features [18••,31]. Performance on these tasks may be severely impaired in brain-damaged patients with parietal lesions ([32]; although see [33]). The critical role of the parietal cortex in the attentional circuit has been confirmed by a study showing that transcranial magnetic stimulation (TMS) applied to the right parietal cortex of normal subjects leads to increased reaction times for conjunctive but not for simple feature searches [34••]. The disruptive effects of TMS, however, can be eliminated by training subjects on the conjunctive visual search task [35•], again suggesting that, as with focused spatial attention [20••], the suppressive effects of the competition can be reduced. Importantly, the benefits of training did not transfer to an isomorphic search task for conjunctions of different features; this suggested that

practice resulted in the bottom-up strengthening of specific connections between representations of the features in the conjunction rather than an alteration in the attentional process (which, presumably, would have transferred to a new stimulus set).

Endogenous biases may also affect the competition in different cortical regions. Even when the visual display is held constant, increased cortical activation in MT–MST was observed when subjects were instructed to attend to moving rather than stationary dots [36]. Under similar conditions, attentional modulation can also be observed in early visual areas such as V1 and/or V2 [37], albeit to a lesser extent [38]. Similarly, enhanced activation is observed in regions of temporal cortex involved in face processing as a function of preferentially attending to faces [39]. Finally, long-latency field potentials in posterior fusiform gyrus, recorded directly from the inferior surface of the temporal lobes in epilepsy patients, are modulated when subjects attend to one of two streams of words [40].

Modulation of competition by object representations: spatially invariant or spatiotopic?

The finding that object representations can alter selection may be readily understood as resulting from interactions between lower-level input representations in early visual cortex and higher-level representations of object structure in the ventral pathway. While some have argued that the object-based attentional effects are mediated by spatially invariant object representations [15], others suggest that they are mediated by more spatiotopic representations (e.g. the 'grouped array' proposed by Farah [41]), and susceptible to modulation by perceptual organization [42•]. Both types of representations, however, probably play a role (see Figure 1). Certainly, it is likely that object perception involves competitive interactions between spatially invariant object representations in later temporal lobe regions (see e.g. [43,44]) and that these dynamics play an important role in determining which of several objects ultimately 'captures' attention and allows for the generation of a behavioral response. However, given the interconnected nature of the visual system, it is also highly likely that these processes influence competition in lower-level visual areas via feedback connections as well as via connections with spatial representations in the dorsal stream (which, in turn, provide biasing feedback to early visual areas). Evidence to support this highly interactive system comes from a study showing that information about visual shape can even affect activity in the parieto-occipital sulcus [45]; magnetoencephalography (MEG) alpha rhythms in this region were suppressed most strongly when participants correctly identified a stimulus as a well-formed object but were enhanced when participants incorrectly labelled objects as noise stimuli and were enhanced even further when stimuli were actually non-objects.

The effect of object properties on single-cell activity can be observed in even the earliest cortical visual areas. Roelfsema *et al*. [46••] found that the firing rates of neurons in V1 corresponding to various segments of a curved line were enhanced relative to responses to a distractor line even when the lines were spatially overlapping. These results suggest that it is the entire object that is modulating the firing rate rather than attention spreading across spatial positions occupied by the curve. The suppression of early ERP waveform components in human subjects also suggests that modulation of early ERP activity may be related to feedback from spatially invariant representations. Because suppression of P1 and N1 ERP components — both of which reflect the spatial distribution of attention — was observed when subjects attended to two different objects that occupied the same spatial position but not when a single object was present, an object-based rather than space-based explanation is more appropriate [47•].

Selection appears to involve not only object-based but also space-based representations. Enhanced amplitude of N1 or P1 ERP signals is seen when subjects report attributes of two overlapping objects [48•]: enhanced N1 signals are observed during trials in which attributes to be reported (e.g. colour and shape) appear in different objects (attributed to a change in the size of the attended region), whereas enhanced P1 activity is observed on same-object trials in which a probe appears after stimulus offset (reflecting the increased focus of attention). Importantly, along with these spatial modulations, enhanced P3 waveforms (a later, more cognitive component) are observed in occipital, parietal, and temporal sites, suggesting the involvement of object-based representations.

The joint contribution of both space- and object-based attentional systems is also evident in a recent PET study. Fink *et al*. [49•] found that there is a substantial overlap in activation of cortical regions when subjects perform an object-based (e.g. is dot on the left or right side of a line?) and space-based (e.g. is the line on the left or right side of the screen?) task relative to a control condition. In addition, there were areas that were selectively activated in each of the two tasks. Areas of overlap included left and right medial and lateral parietal cortex, as well as left prefrontal cortex; however, the left occipital lobe, and the striate and prestriate cortex were activated only in the object-based task, and the right inferior temporal lobe, fusiform gyrus, and right dorsolateral prefrontal cortex were activated only in the space-based task.

The interactions between perceptual organization of objects and spatial attention are also evident in studies of patients who extinguish left-sided information following right-parietal lobe damage. Just as a prior temporal entry for a contralateral target can reduce the probability of its being extinguished by a competing ipsilateral target [23••], so can grouping the contralateral item with its ipsilesional counterpart makes it resistant to extinction. Left-sided information can be grouped with right-sided information by bottom-up factors such as colour, proximity, brightness or collinearity [50,51], or even by an illusory contour of a partially occluded figure [52•]. Top-down modulation also plays a role, resulting in less extinction for known, familiar objects or words than for unknown items [53–55].

Computational accounts and integrated competition

Several recent computational accounts of visual attention include an attentional map (also referred to as a priority or saliency map [8,56]) that instantiates the WTA dynamics. The winner, which emerges from the competition, may then be mapped through a smaller 'attentional' window (the selection network [57]) or may be selected as the target because of its high saliency value (both absolute and relative to the other stimuli [58•]). Selected representations may be subsequently inhibited to implement inhibition of return [58•]. These models successfully simulate not only the performance of normal subjects in various experimental paradigms, but also exhibit the behavioral pattern associated with attentional deficits such as hemispatial neglect and extinction. One notable difference between these models and the full integrated competition account is that in the models the competition is more localized to a particular component rather than being widespread throughout the processing circuit. Whether this departure is truly significant remains to be determined.

Conclusions and future directions

Behavioral and neurobiological data are increasingly converging on the notion that selecting a target from a complex array of visual stimuli involves a recurrently connected network of visual processing areas. Competition and cooperation of units in this network facilitate the emergence of a winner from a host of potential targets. While we know that the competition can be modulated, and we know some of the characteristics of this modulation, a full understanding of the factors that bias the outcome and the mechanism by which this occurs remains to be determined. Of importance too are the variables that potentially cancel out the suppressive interactions and the time course of the competition and its consequences.

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The authors made ERP recordings while subjects reported the presence or absence of a pair of attributes (a colour and a shape) in displays consisting of two overlapping line drawings; probe dots occasionally appeared subsequent to the removal of these displays. Data revealed enhanced ERP waveforms indicative of early, space-based attention when both objects contained a target attribute (larger N1) as well as when probe dots appeared in locations previously occupied by objects containing both target attributes (larger P1).

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The major focus of these simulations is the representation of space using mathematical basis functions (roughly analogous to dimensions or co-ordinates) of sensory inputs. A saliency value assigned to the inputs, however, determines selection, and once a position is selected, its saliency is subsequently set to zero (and return to it is inhibited). A range of data from patients with parietal lesions is simulated under these computational conditions. Use of basis functions provides an explanation of how multiple attentional deficits can be evoked by a single lesion to a neural network.