

Competitive brain activity in visual attention

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Visual attention can be considered from the perspective of distributed brain activity engendered by visual input. We propose that visual objects compete for representation in multiple brain systems, sensory and motor, cortical and subcortical. Competition is integrated, however, such that multiple systems converge, working on the different properties and action implications of a selected object. Top-down priming biases competition towards objects relevant to current behaviour. Recent single-unit studies have shown widespread suppression of ignored-object representations in extrastriate cortex, and patterns of spatial and nonspatial priming by task relevance. Human and monkey lesion studies have demonstrated the strong integration tendency of different spatial and nonspatial systems, also revealed in recent studies of normal behaviour. In many cases, no unitary brain system may be responsible for unitary cognitive events such as attention. Such events may emerge as distinct systems converge to work on common cognitive problems.

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Abbreviation

SLAM selective attention model

Introduction

Multiple brain systems are concurrently activated by visual input. In the primate brain, these include the multiple cortical 'visual areas', specialized for different purposes and, at least in part, for the analysis of different visual attributes, such as motion, spatial arrangement and shape [1,2]. Among visually responsive subcortical structures are the superior colliculus, which is involved in multimodal orienting [3], and several subdivisions of the pulvinar [4]. Among motor systems activated by visual input are premotor cortex, which is important in reaching and grasping [5], and the frontal eye fields and associated structures [6], which are involved in oculomotor control.

In this review, we consider the problem of selective visual attention from such a perspective of distributed brain activity. In our cluttered visual world, only a small part of the total visual input can be used at any given time in the active control of behaviour [7,8]. Subjectively, attention is focused on a part of the input at the expense of the

remainder. We consider how such selectivity is achieved in the distributed network of brain systems activated by visual input. This is a restricted review, presenting a specific hypothesis—the integrated competition hypothesis—and relevant experimental work, including studies of single-neuron activity in the behaving monkey, attentional impairments after brain lesions, and normal attentional function. More detailed treatments are available [9,10], building on ideas introduced by Desimone and Duncan [11]. Other aspects of attentional function have been reviewed recently elsewhere [12].

The integrated competition hypothesis

The integrated competition hypothesis rests on three general principles.

First, many brain systems, sensory and motor, cortical and subcortical, are activated by visual input. Within many and perhaps most of these systems, activations from different objects compete. A gain in activity for one object is accompanied by a loss in activity for others.

At the behavioural level, competition between objects is manifest as interference in their joint processing. Many experiments have detailed the interference that occurs when properties of two different objects must be identified concurrently. This interference occurs whether objects are at widely separate spatial locations or overlapping on the fovea [13,14], and lasts across a few hundred milliseconds of temporal separation [15,16]. Experiments have also detailed the suppressed processing of ignored objects [17].

Second, though competition takes place in multiple brain systems, it is integrated between systems. As a winning object emerges in one system, it tends also to become dominant in others [18,19]. For the sensorimotor network as a whole, the tendency is to settle into a state in which different brain systems have converged to work on the same dominant object, analyzing its multiple visual properties and implications for action. This is the state that, at the behavioural level, corresponds to 'focused attention' on the selected object. At the neural level, there should be widespread maintenance of the selected object's representation, accompanied by widespread suppression of response to ignored objects.

In behavioural studies, the interference found when properties of two different objects must be identified vanishes if the task is, instead, to identify two different properties of the same object [13,20]. Thus, directing attention to a selected object makes its different features available together for control of behaviour and verbal report.

The central role proposed for integration raises the question of how such integration might be achieved. If colour and motion, for example, are processed in somewhat separate extrastriate systems, what scheme would encourage the same object to achieve dominance in both areas (cf. the conventional binding or feature integration problem [21])? Without commitment to any particular one, we may note that several solutions have been proposed. The SLAM model of Phaf *et al.* [19], for example, incorporates separate modules for individual visual features, such as colour, location and form, along with pairwise conjunction modules for, for example, colour and location or colour and form. Consider a display containing a red O on the left and a green X on the right. As soon as dominance is achieved in any one module (e.g. red units become dominant over green within the colour module), corresponding units are supported and tend to become dominant in conjunction modules (red O units over green X units, red left units over green right units); a pattern that is, in turn, transmitted to other single-feature modules (O units become dominant over X units, left units over right units). Irrespective of the details, the general idea in such models is that, directly or indirectly, units responding to the same object in different modules support one another's activity, whereas units responding to different objects compete. The strength of the integration tendency will depend on the strength of the between-module support by comparison with other influences. Such a scheme has properties necessary for the principles of integrated competition.

Third, competition can be directed on the basis of relevant object properties. Undoubtedly, there are enduring or bottom-up biases towards objects that are moving, bright, large and so on [22,23], but, in general, it must be possible to select any kind of object for control of behaviour, depending upon the current task demands. We suggest that task-specific selection is controlled by top-down neural priming [24,25]. Suppose that a person is told to search for objects of a particular colour. Units responding to that colour are primed in one or more systems within which colour is coded. Objects of the desired colour then gain a competitive advantage in the primed system. In accord with the principles stated above, as the object gains control in the primed system, it tends also to take control of others. The end result should be a generalized ascendancy of the desired object in multiple systems, making its different properties concurrently available.

Flexibility of selection is a requirement of normal vision: many different features can be used to direct attention to those objects of relevance to a current task. For example, subjects can be asked to read just the letters in a certain row of a briefly presented array (selection by location) [26], just the letters of a certain colour or size (selection by object feature) [27], or just the letters and not the digits (selection by category) [28]. In all these cases, irrelevant or nontarget characters are quite successfully ignored; for

example, the number of nontargets in a display has little effect on target identification [29,30]. According to our hypothesis, such flexible selection rules are implemented by flexible, task-specific patterns of top-down neural priming in multiple sensorimotor areas.

Attentional modulations in the extrastriate cortex of the macaque

Single-unit studies in the behaving monkey have shown how the behavioural relevance of a stimulus can modulate the neural response it produces [31]. Early studies showed stronger responses to relevant (attended) than to irrelevant (unattended) stimuli in a range of tasks and higher visual areas, including posterior parietal cortex [32], which is important in spatial vision and the control of spatial behaviour [33,34], and occipital (V4) and temporal (IT) areas, which are involved in feature and object recognition [35]. Recent studies have further developed these initial observations.

A number of these studies have used spatial selection tasks [36**–38**]. In a typical task, a cue indicates the relevant location for a trial or series of trials. For example, the monkey might be required to make a shape or other discrimination at the cued location. Following a delay, displays are shown, including stimuli in both cued and uncued locations. There is typically one 'effective' stimulus to which the recorded cell is responsive, that is, a stimulus positioned within the receptive field and with appropriate sensory properties. Cues are manipulated so that on some trials the effective stimulus is relevant, whereas on others it should be ignored. Responses to the effective stimulus are compared under these two different attentional conditions.

Converging evidence from such spatial selection tasks suggests the following conclusions. First, in the delay period between cue and display, when no stimulus is actually present in the receptive field, 'spontaneous' or background activity can depend on the cued or relevant location. Enhanced activity when the cued location lies within the receptive field has been observed in both V2 and V4, though, interestingly, it was not found in V1 [36**]. Cue locations at different positions within the receptive field have also been compared: in general, the more responsive a cell is to stimuli in a given location, the more delay period activity it will show when that location is cued. Second, when an effective stimulus is present in the receptive field, the cell's response depends on the attentional state. By comparison with responses to attended stimuli, suppressed responses to unattended stimuli have been reported in numerous visual areas, now including the motion-sensitive areas MT and MST [37**], in addition to V2 [36**], and V4, IT and posterior parietal cortex, as already discussed. In a systematic study of proximity between a presented stimulus and the attended location, Connor *et al.* [38**] have found increased V4 responses with increasing proximity. An interesting further

observation in this study was that, irrespective of stimulus position, a cell's responsivity could depend on the absolute position of the cued location outside the receptive field.

In nonspatial selection tasks, the relevant object is indicated not by its position but by its identity or other features. In a study by Chelazzi *et al.* [39], the cue was a complex object shown at fixation. Following a delay with only the fixation point present, an array of 2–5 objects was shown in the periphery, and the monkey was required to make an immediate saccade to the object matching the initially presented cue. In IT, where cells are selectively responsive to particular objects or their features, there was selective activity in the delay period, now dependent not on location but on target identity. Cells responsive to the current target showed enhanced activity (see also [40,41]). When the array was presented, results matched those seen in spatial selection tasks: responses to the relevant or target object were strong and sustained, whereas after an initial discharge, responses to nontarget objects were suppressed.

Taken together, these results support two predictions of the integrated competition hypothesis. First, even in the absence of a visual display, neurons responsive to task-relevant inputs show enhanced or primed activity. Depending on whether relevance is defined by location, by identity or, presumably, by other features, very different patterns of priming will occur, very probably in different extrastriate systems. Second, these different patterns of delay activity lead to a comparable final result when a display of several objects is presented; there is widespread suppression of ignored-object responses, probably affecting much of the extrastriate cortex.

Several authors have suggested that backward projections from later to earlier visual areas may serve an important role in solving the integration problem (see e.g. [42*]). If responses to irrelevant objects can be suppressed in an early visual area, all systems receiving an input from that area will follow suit. This form of integration can be readily demonstrated in systems such as the SLAM scheme outlined above. For example, IT cells could support the activity of cells with congruent feature preferences in the earlier area V4, so that dominance of a particular object representation in IT would lead to dominance of matching-feature representations in V4. Data consistent with this possibility were obtained by Chelazzi and Desimone (L Chelazzi, R Desimone, *Soc Neurosci Abstr* 1994, 20:1054) in the object search task. In this task, V4 cells showed little selective delay activity, suggesting little local priming of units responsive to target object features. Despite this lack of priming within V4 itself, suppression of nontarget responses developed once the search array was presented and the animal prepared for a saccade.

For many visual inputs, however, considerable doubt exists regarding how early in the visual system suppression of

responses to irrelevant or nontarget stimuli will be seen. In V4, Moran and Desimone [35] found suppression only when attention had been withdrawn from the effective stimulus to another, ineffective stimulus within the cell's receptive field. This finding has been recently confirmed by Luck *et al.* [36**] and extended to V2. Smaller receptive fields at earlier levels of the visual system will make it less likely that relevant and irrelevant stimuli both fall within them and less likely, accordingly, that responses to irrelevant stimuli are suppressed. In these studies, indeed, the responses of V1 cells were unaffected by attention [35,36**], perhaps because simultaneous stimuli could not be fitted within a single receptive field while maintaining the animal's performance. Some other studies have confirmed that attentional modulation is strongest when competing stimuli lie within the receptive field [37**]; at the same time, some modulation has been reported both in V1 [43] and elsewhere, even when this condition is not met ([37**,38**] and, especially, [44]). Suppression of nontarget responses may be stronger when an experiment uses complex, cluttered displays ([43]; though see [36**]). It may also be stronger when long stimulus exposures give time for attention to be clearly focused, or, in terms of the integrated competition view, for the network to settle into the required dominance state. In Motter's [44] study using long stimulus exposures, maximal nontarget suppression took several hundred milliseconds to develop, a duration longer than total stimulus exposure in many studies. More work will be needed to resolve these issues.

Though the emphasis in this section has been on extrastriate activity, there are doubtless broader influences on both priming and between-object competition. Directly linked to IT cortex is the inferior convexity of the frontal lobe, and here recent data from monkey neurophysiological studies suggest pronounced delay-period activity during an object search task (L Chelazzi, EK Miller, A Lueschow, R Desimone, *Soc Neurosci Abstr* 1993, 19:975; see also [40]). In analogous spatial tasks, strong delay activity has been observed in both dorsolateral prefrontal and premotor cortex [45,46]. Relations between frontal and posterior systems remain to be clarified, along with their joint role in guiding attentional competition.

Spatial integration

A part of the integration problem is the need for multiple systems to work together on the same area of space [47–49]. Relevant studies concern spatial disorders following brain damage and spatial integration in normal cognition.

Because the brain's representation of space is predominantly crossed, unilateral lesions commonly produce deficits in registering and interacting with events on the opposite side. A competitive element to these disorders is shown by the phenomenon of unilateral extinction: though the patient may respond well to a single stimulus in

contralesional space, this stimulus is disregarded or poorly identified in the presence of simultaneous, ipsilesional input [50]. Extinction is especially strong when the ipsilesional object itself is relevant to behaviour [51]. Such results suggest biased attentional competition towards the ipsilesional side [52].

As noted above, a general distinction may be drawn between an occipitoparietal processing stream, which deals with spatial relations and visuomotor behaviour, and an occipitotemporal stream, which deals with object features and object recognition [33]. Extinction has sometimes been seen as a part of the broad pattern of spatial deficits produced by parietal lesions, and, therefore, specifically associated with those lesions [53]. A different view is suggested by the integrated competition hypothesis. Once an object becomes dominant in any one part of the sensorimotor network, it will tend to capture control of the network as a whole. Given that unilateral lesions in many different parts of the sensorimotor network weaken the local representation of contralateral space, they should produce a common extinction tendency.

Several lines of evidence are consistent with this prediction. In an early monograph, Bender [50] described extinction following many different lesions weakening a part of the sensory input. For tactile inputs, even lesions of the peripheral nerves or spinal cord were sometimes effective. Confirming these results, a recent large series study [54] has shown visual extinction following a broad range of cortical and subcortical lesions. In individual cases, very similar extinction has been described following parietal and occipitotemporal lesions [9*]. Data from studies on monkeys suggest a similar conclusion. In one study, the feature discrimination deficit consequent on a V4 lesion was severe only when the object falling in the impaired region of the visual field was accompanied by an irrelevant distractor in an unimpaired region (R Desimone, L Li, S Leaky, L Ungerleider, M Mishkin, *Soc Neurosci Abstr* 1990, 16:621). Similar results follow lesions in a variety of cortical and subcortical structures, including the superior colliculus and the lateral pulvinar [55]. Many spatial deficits may indeed be specifically associated with parietal lesions, including the broad pattern of 'neglect' measured in many tests of contralesional representation and exploration [56]. The simple element of competitive bias in these deficits is, however, a common consequence of many different unilateral lesions.

Interestingly, a number of different local biasing inputs have been used in recent treatment studies aiming to diminish the symptoms of unilateral neglect. To the extent that neglect has a component of competitive imbalance, our hypothesis implies that it might be corrected by many different forms of local processing bias inducing a global competitive shift to the neglected side [47,57]. Correspondingly, relief of left-sided neglect has been obtained by requiring irrelevant movements of the left hand in

left space [58], by patching one eye to bias collicular inputs [59], by vestibular stimulation inducing leftward orienting [60], and by a range of other forms of lateralized stimulation. Doubtless, these different procedures have direct effects on very different lateralized systems; the end result, however, is a generalized competitive shift. The results provide strong evidence that lateral biases are integrated across multiple sensorimotor systems.

Studies of normal function provide numerous similar examples. Morais [61], for example, has shown that focusing attention on an auditory stimulus from the left is favoured by turning either eyes, or the head, or even the trunk in that direction. Recent studies have shown how lateralized attention in several sensory modalities can be biased by inputs from another modality [62*], by proprioceptive and postural factors [63**], and by preparation for targeted movements of eyes or hand [64*,65**]. At the same time, exceptions to generalized spatial integration should also be noted [66]. As one example, Spence and Driver [67*] have found that irrelevant lateralized auditory inputs bias visual attention, but not vice versa. The findings of dissociated neglect in different modalities [68], or of dissociated sensory and motor neglect [69], similarly show that the tendency to spatial integration is not absolute. Conditions encouraging relatively strong or relatively weak integration between distinct spatial systems have not yet been clearly established.

According to the integrated competition hypothesis, the sources of spatial bias considered above must be combined with assorted nonspatial factors to determine the final pattern of object dominance. Nonspatial influences on extinction have been documented in a number of recent studies. Ward and Goodrich [70**], for example, have shown that a nonsense drawing in the contralesional field is more likely to be extinguished than a drawing of a familiar object, even though the task is simply to detect the presence of any stimulus. This result suggests a competitive advantage for familiar shapes (see also [71*]). Other nonspatial influences on extinction include bias towards closed rather than open figures [72] and towards contralesional inputs linked by strong Gestalt grouping factors to attended ipsilesional material [10*,52,73*]. More generally, effective behaviour of many different kinds demands integrated selection of relevant goals, action plans, and sensory inputs [74]. As an example, one recent study [75**] provides evidence that the degree of unilateral neglect depends on the purpose of a manual response (grasp or balance versus point). Thus, spatial bias is only one of many factors influencing the broad problem of unbalanced attentional competition following brain lesions.

Conclusions

The integrated competition hypothesis relates general requirements on an attentional system to data concerning single-neuron activity in the macaque, spatial and non-

spatial influences on extinction following brain lesions, and integrative processes in normal sensorimotor cognition. According to the hypothesis, there is no localized system responsible for visual attention: even functional components (priming, competition and integration) have no distinct localization. Instead, selection of objects for the control of action arises through cooperative and competitive activity across multiple brain systems. At the same time, the hypothesis imposes severe limits on parallelism. In line with the restrictions on parallel processing obvious in everyday behaviour, integration severely restricts the ability of multiple brain systems to work concurrently on different tasks. Visual attention provides a well worked-out example of these general principles. It will be interesting to see how widely they apply to other forms of higher cognitive activity: for example, to joint activity of different motor systems in action selection or to combination of phonological and semantic systems in word production [76]. In many cases, no simple mapping may exist between unitary cognitive events and unitary neural systems.

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