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Vision: Attention Makes the Cup Flow Over

Scalp potentials are surprisingly informative about visual attention: a recent study that used them to record neural responses to up to four superimposed visual patterns simultaneously has now revealed the flow of attentional signals back to visual cortex.

Jochen Braun and Mircea Ariel Schoenfeld

When we fix our gaze on a complex visual scene, we can alter our phenomenal experience by focussing mentally on different parts or aspects of the scene. Neural correlates of this 'selective visual attention' have been observed in an anatomically distributed, but functionally integrated, network of brain sites, including the lateral geniculate and pulvinar nuclei of the thalamus, visual areas in occipital and temporal cortex, and higher order areas in frontal and parietal cortex [1,2]. It is thought that attention signals originate in frontal and parietal cortex and are then transmitted by feedback and recurrent projections backwards to earlier stages of the visual pathways. These efferent signals seem to selectively enhance the amplitude, and perhaps also the temporal synchronicity, of neural responses to the 'attended' parts or aspects of a visual scene, at the expense of the neural responses to all other parts or aspects of the scene.

Except in the most simplistic displays, however, the attentional enhancement of neural responses is not limited to the desired information, but extends also to some other stimulus features that may be present in the display but that are irrelevant to the task at hand. This 'spill-over' to some irrelevant features (but not to others) is of considerable interest, as it presumably reflects the organization of the projection patterns that communicate attentional signals back to visually responsive neurons.

One pattern of spill-over goes by the name of 'object attention'. Typically, object attention is encountered when two visual patterns are superimposed transparently, that is, such that each pattern remains recognizable individually. To take an idealized example, an array of red items moving coherently in one direction might be superimposed over an array of blue items moving coherently in another direction (Figure 1A). Because of the shared colour and motion, each array is phenomenally experienced as a distinct visual object. In viewing such a display, observers can choose which array they attend and, thus, which array they experience more fully.

Attentional spill-over becomes apparent when observers are asked about one particular attribute of one array, the shape of the red array items. In this case, the attentional enhancement — as measured either behaviourally or neurophysiologically — applies not only to the relevant attribute (shape) but also to the irrelevant attributes (motion, colour) of the target array. All attributes of the other array are suppressed, however. Thus, in this simplified example, object attention enhances all responses to the attended array and suppresses all responses to the unattended array.

Object attention has been documented most extensively with purely behavioural measures [3–6], although a few studies have encountered its characteristic pattern of spill-over enhancement also in single-unit activity of visual cortex [7] and in visual evoked potentials [8,9]. Note that electrophysiological studies of attentional spill-over face an enormous hurdle: they must distinguish the neural responses not just to two superimposed patterns, but to relevant and irrelevant attributes of these patterns.

Over the last decade, the measurement of visual evoked potentials on the scalp has been refined to the point that it can now overcome this hurdle. A key to the singular informativeness of this method is the oscillatory response evoked by a flickering pattern that is known as a 'steady-state visual evoked potential' or SSVEP [10]. As the frequency of the oscillatory response matches that of the driving flickering pattern, two patterns flickering at different frequencies elicit distinguishable oscillatory contributions to the visual evoked potential. When observers are required to discriminate one pattern, the neural response to the attended pattern (as measured by the SSVEP) increases relative to the response to the unattended pattern [8,9,11].

As they reported recently in *Current Biology*, Andersen *et al.* [12] have been able to distinguish neural responses to *four* superimposed arrays, setting a new standard for evoked potential methods and affording an even more penetrating insight into attentional

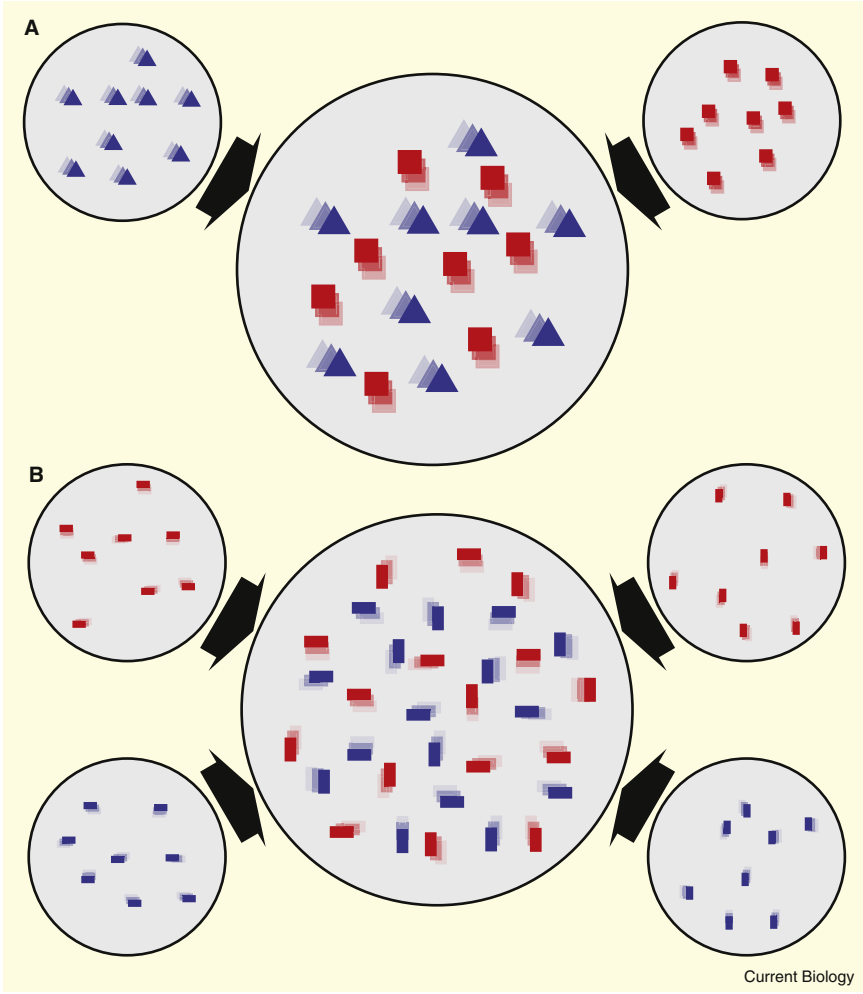

Figure 1. Object and feature attention.

(A) Typical demonstration of object attention (idealized after [5,9]). Two arrays are superimposed (blue triangles moving right and down, red squares moving up and left), which observers perceive as phenomenally distinct visual objects. (B) New demonstration of feature attention by Andersen *et al.* [12]. Four arrays are superimposed (red/horizontal, red/vertical, blue/horizontal, and blue/vertical), with each item moving in an arbitrary direction. As the arrays are distinguished only by a combination of features (rather than by any single feature), they do not form phenomenally distinct visual objects.

spill-over. In their study, each of the four arrays was formed by items with a particular combination of colour and orientation and was flickered with a distinct frequency (Figure 1B). Thus, no single feature distinguished each array: colour and orientation were shared with another array and the motion of array items was uniformly incoherent. Accordingly, observers could not phenomenally experience each array as a distinct visual object.

Observers were induced to attend to one particular array, that is, to a particular combination of colour and orientation. As each array was tagged with a distinct frequency, the neural response to each array could be gauged by its specific SSVEP. Consistent with previous findings, the response amplitude of the array with the attended colour and orientation (for example, red-horizontal) was enhanced relative to the array with unattended colour and orientation (for example, blue-vertical). The novel finding was that the attentional enhancement 'spilled over' to the arrays with one attended and one unattended feature (for example, red-vertical and blue-horizontal). In short, attention enhanced the responses to task-relevant features wherever they were present in the display, making no distinction between different arrays.

The pattern of attentional spill-over in the results of Andersen *et al.* [12] is known as 'feature attention'. Feature attention has been observed behaviourally [13], in single-unit activity [14], and with functional imaging methods [15–17], generally in displays that do not segment into phenomenally distinct visual objects. The prototypical situation for demonstrating feature attention is a visual search: a target item, which the observer attempts to locate, is defined by a combination of features and each individual target feature is present also in distractor items. In this situation, neural responses to distractor items sharing target features tend to be enhanced relative to distractor items not sharing target features [18].

So what does this tell us about how the task-relevance or -irrelevance of a visual attribute modulates neural responses to this attribute? Clearly, the pattern of attentional enhancement seems to depend on circumstances: the enhancement is restricted to the task-relevant visual object when the display segments phenomenally into such objects, but spreads to task-relevant features everywhere when the display does not support segmentation into objects. The crucial question would now seem to be the relative timing of the different kinds of enhancements. Does feature attention consistently precede object attention in time, so that the two form successive steps toward building-up the eventual pattern of attentional emphasis on visual responses? Or do feature and object attention constitute separate mechanisms and build-up over different time-scales that depend on the nature of each display? Several studies have demonstrated the feasibility of discerning the relative timing of different kinds of attentional enhancements [8,15,19,20]. In view of their astonishing discriminative powers, visual evoked potentials will surely continue to play a leading role in answering these questions and in further unravelling the various mechanisms of visual attention.

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Intracellular Transport: Kinesins Working Together

While most *in vitro* experiments with motor proteins focus on the behavior of individual motors, in cells most cargo are transported by multiple motors and even multiple classes of motor. How these motors cooperate and compete in transporting cargo is not clear. Recent experimental and theoretical work suggests that motors attached to a given cargo interact in both expected and unexpected ways.

William O. Hancock

Microtubule-based transport of intracellular cargo, such as vesicles and organelles, is carried out by kinesin and dynein motor proteins. Experiments in cells have helped to define which motors move which cargos, while single-molecule investigations have defined many of the performance characteristics and underlying mechanisms of individual motors. What is less clear is how multiple motors attached to a cargo interact mechanically to achieve long-distance cargo transport that can withstand significant viscous and elastic loads.

One characteristic of transport motors is their processivity — their ability to walk multiple steps along their filament track without detaching. Clearly, having multiple motors attached to a given cargo will increase the cargo's transport distance because, when one motor detaches, other motors will maintain association with the track. How the forces of multiple motors sum is somewhat less clear — are forces shared equally by all motors such that the maximal load a cargo can move against is simply a multiple of the single-motor stall force, or is the relationship more complex? And intuition really starts to be taxed in predicting the force–velocity relationship of a cargo transported by multiple motors. Under load, do a fraction of the motors become particularly taxed and slow down the group, or do cooperative phenomena minimize load-induced slowing?

These questions are important for understanding the workings of motors in cells. For instance, in bidirectional transport, as seen for melanosomes, intraflagellar transport and axonal transport [1,2], how many motors need to be turned on or off to trigger directional switching? And what sorts of regulation and cooperative interactions underlie the complex oscillations of chromosomes seen during metaphase? While understanding the characteristics of the individual motors involved in these processes is important, there is clearly another level of complexity that needs to be considered when developing realistic physical models of these processes.

Current efforts to attack these questions rely on a paired approach of *in vitro* experiments using cargos functionalized with many motor proteins and theoretical models that extrapolate from single-motor to multi-motor behavior. In this issue of *Current Biology*, Kunwar and colleagues [3] describe a mechanochemical model consisting of two, three, and four kinesin motors attached to a rigid cargo. The model builds upon previously developed models of single motors [4,5] and, importantly, includes a compliant linker domain that connects the motor domains to the cargo. Individual motors are allowed to independently step along the microtubule and the position of the cargo is tracked. Loads are imposed on individual motors both from random variations in the stepping rates that cause the motor–cargo linkages to stretch, and from external loads imposed on the cargo (as in optical-trapping experiments).

An important innovation in the Kunwar model [3] is the approach to load sharing. In an earlier model of multi-motor transport, Klumpp and Lipowsky [6] assumed that the load was shared equally by every attached motor. A more realistic picture is that,