Visual Attention: Light Enters the Jungle

Dispatch

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Recent studies focusing on basic visual attributes, such as luminance, colour and motion, are providing a starting point for investigating the relationship between perceptual and neural manifestations of attention.

Although the nature of selective attention remains one of the knottier conundrums of perception research, some aspects of this tangle of problems are now approaching a pleasing state of clarity. It is now quite evident that directing attention to a visual stimulus changes neural responses to that stimulus throughout the visual cortex [1], and that these widespread neural changes affect, unsurprisingly, many aspects of visual function. Perhaps most consequential is the influence that attention wields over the contents of visual awareness and, thus, over all the post-perceptual processing that awareness entails - short-term memory, perceptual decisions, voluntary responses and so forth. In fact, awareness seems to follow attention so inexorably that there is a temptation to equate the two, but a closer look yields a good crop of counterexamples [2].

Another major effect on visual function is that attention appears to enhance and augment the mental representation of visual stimuli in quantitative and qualitative ways. This 'signal enhancement' manifests itself in a variety of ways, including accelerated reaction times, improved sensitivity (thresholds) [3,4], reduced interactions with flanking stimuli [5,6], and elimination of illusory conjunctions [7]. Finally, attention allows visual decisions to be based on the selected stimulus alone and thus to disregard any distracting stimuli which may be present. Accordingly, attention is often said to increase 'positional certainty' [8]. Of course, these manifold manifestations of attention - awareness, signal quality, positional certainty - may well be closely interrelated and connected. Indeed, visual selective attention is thought to exhibit many of the hallmarks of an integrated, all-or-none process.

A new study by Morrone *et al.* [9], published recently in *Current Biology*, focuses on 'signal quality' with respect to luminance and colour contrast. The perception of contrast can be precisely quantified, and although the neural basis is not yet known with certainty, there exist plausible candidate pathways for both luminance and colour contrast in visual cortex [10–12]. Thus, the most basic of all visual attributes contrast — presents an excellent opportunity for linking perceptual and neural manifestations of attention. Morrone *et al.* [9] measured 'increment thresholds' for both luminance and colour contrast, that is,

Institute of Neuroscience, Plymouth, Devon PL4 8AA, UK. E-mail: achim@pion.ac.uk they determined how far each type of contrast must be raised above a given baseline level for the difference to be distinguished. They repeated their measurement of 'increment thresholds', in which a large grating pattern appeared either side of fixation, three times, for both types of contrast, coaxing the observer's attention into a different state each time. The coaxing was done by a visual search near fixation, which the observer was obliged to carry out as an additional, concurrent task (an effective and reliable way to control allocation of attention [2]).

The special twist applied by Morrone *et al.* [9] was that, just as with the contrast task, the visual search also involved either luminance or colour contrast the search targets differed from non-targets in either luminance or colour contrast. With this twist, the authors were able to compare three distinct states of attention: attention divided between tasks involving the same type of contrast; attention divided between different types of contrast; and attention focussed on the grating pattern (whilst the visual search is ignored).

Among the several intriguing contributions of this study, the sheer size of the observed effects of attention takes first place. When attention was focussed, the measured threshold increments of luminance and colour contrast were approximately 30-70% lower than when it was divided (between same types of contrast), implying a correspondingly large improvement in the signal-to-noise ratio. To put this in perspective, we can compute how much the contrast gain of a hypothetical neuronal population would have to increase in order for the signal-to-noise ratio to improve to this extent. Morrone et al. [9] calculate this to be an approximately two-fold increase in contrast gain. This may be an underestimate, however, as it assumes a response variance that is independent of the response mean, whereas the response variance of cortical neurons grows roughly in proportion to the mean.

The results of Morrone et al. [9] may thus actually indicate that focused attention confers as much as a four-fold increase in the contrast gain of neuronal populations encoding luminance and colour contrast [13]. Although this figure may seem implausibly large, it is well in line with earlier studies of attention effects on contrast thresholds [4]. Matching these large threshold differences to correspondingly large changes in neural activity is complicated by the vast difference in paradigms and by uncertainty about the exact neuronal substrate of luminance and colour perception. In visual cortical areas V1 and V2, where functional imaging studies show that BOLD activity correlates reasonably well with psychophysical sensitivity to luminance [14] and colour contrast [15], the size of attention-induced changes in BOLD activity can reach at least 25-40% of the size of stimulus-evoked changes [16,17]. However, the neural substrate of perceived contrast must presumably be sought in subpopulations of early visual cortical areas, such as the



Figure 1.

Two alternative ways of interpreting the findings of Morrone et al. [9]. Schematic illustration of the four different visual displays used (LL, CC, LC, CL) and of possible distributions of attention. A visual search array (colour or luminance search) is at the centre of each display. In the search task, observers report on an array element of distinct colour or luminance: is it present or absent? Two grating patterns (colour or luminance) appear on either side of the search array. Observers compare the grating contrast - is it higher left or right? - in order to measure sensitivity for colour/luminance contrast. When observers perform both the search and grating tasks, contrast sensitivity deteriorates in the CC and LL cases, but remains unchanged in the CL and LC cases. This is indicated by the red Xs or Vs on the right margin. Why should focussing attention on the search have this differential effect? (A) Morrone et al. [9] propose two independent 'beams' of attention, one raising sensitivity for colour and one for luminance contrast. If each 'beam' can benefit only one task at a time - either search or grating task but not both then the grating patterns will be unattended in CC and LL, but not in CL and LC situations, explaining the differential outcome observed. (B) Another possibility is a single 'beam' of attention, which may benefit either one task or both. If this 'beam' was focussed narrowly on the search array in CC and LL, but dispersed more widely between search array and grating pattern in CL and LC, this would also account for the results. Such differences in the spatial distribution of attention may result from physical stimulus differences (via grouping interactions).

upper layers of 'inter-blob' regions in area V1 and 'inter-stripe' regions in area V2 for luminance contrast, and upper layers of 'blob' regions in area V1 and 'thinstripe' regions in area V2 for colour contrast (where the blobs, stripes and intervening regions are defined by cytochemical labeling) [10–12]. Finding the large response changes predicted by the psychophysical evidence in such defined populations will most likely require single-unit recording in behaving primates.

Another intriguing aspect of the findings reported by Morrone *et al.* [9] is what they term 'independent attention'. The observation in question is that dividing attention lowers thresholds when the division spans the same type of contrast — colour search and colour grating, or luminance search and luminance grating but not when it spans different types of contrast colour search and luminance grating, or *vice versa*. To account for this observation, Morrone *et al.* [9] propose the existence of two independent 'beams' of attention, one raising sensitivity for luminance contrast and the other sensitivity for colour contrast (Figure 1A).

Assuming that each postulated 'beam' can benefit either one stimulus or the other — search stimulus or grating stimulus — but not both, this hypothesis would neatly explain the results. However, as there is considerable prior evidence that attention is an integrated, all-or-none process [2,18] — a single 'beam' raising sensitivity to all types of threshold — it is prudent to consider whether there may be alternative interpretations. Indeed, one alternative is that there is a single 'beam' which may benefit either one stimulus or the other, or both.

Assuming that physical stimulus differences enforce (via grouping) a 'narrow beam' for the same type of contrast while permitting a 'wide beam' for different types of contrast (Figure 1B), this could account for the results just as well. Parenthetically, it should be noted that both alternatives assume additionally that some visual awareness of either stimulus is mediated by non-attentive processes — the global stimulus competition underlying bottom-up saliency [2,19] — so that a (reduced) sensitivity can be measured even in the absence of an 'attentional beam'.

To decide between these alternatives, one would need independent information as to whether the 'attentional beam' was narrow or wide in the situations under consideration. Typically, a 'narrow beam' can be assumed when concurrent tasks interfere to the point of mutual exclusion, that is, when optimal performance of one task reduces performance of the other task to the level of chance [2,20]. In the present experiment, this was clearly not the case - observers happily performed both tasks well above chance - so that we lack positive proof of a 'narrow beam'. In fact, the experiment of Morrone et al. [9] was deliberately patterned after situations known to yield comparatively modest degrees of interference (which nevertheless translate into very substantial changes in sensitivity) and which thus are relatively uninformative as to 'beam' width.

It is perhaps not too churlish to suggest that attention research remains caught in a thicket of conceptual and methodological confusions, at least as far as more fundamental questions about its computational nature, its neuroanatomical basis in cortex and subcortex, and its implementation in local neuronal circuits are concerned. The new study by Morrone *et al.* [9] points toward an escape route from this predicament: a detailed psychophysical characterisation of how attention changes visual sensitivity and phenomenal experience, followed (hopefully) by the identification of corresponding changes in localised neuronal activity. Basic visual attributes — luminance, colour and motion, for example — for which plausible candidate pathways in visual cortex have been proposed, are the obvious starting points for this route. Although aimed at attention, such endeavours will also illuminate other basic aspects of the neurobiology of vision. One may look forward, in particular, to learning more about the cortical encoding of visual information and perhaps even about the neural basis of visual awareness.

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