

Shifting attention to neurons

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Cavanagh *et al.* [1] challenge the traditional idea that neuronal activity caused by impending saccades alters receptive field (RF) locations. The authors argue, instead, that saccade-related signals cause shifts of attentional pointers that lack information about object identity but influence visual regions that encode object properties. We agree that the relationship between attention and remapping warrants additional study. However, we think that the authors' proposal, although constructive, is incomplete given neurophysiological data.

Attentional allocation and remapping are probably closely related. There is evidence that attention influences the shape of RFs in visual areas MT and V4 [2,3]. A simple extension of this operation might be to move an RF. Also, thinking of remapping as an attention-related process makes sense in terms of timing. Activation transfers caused by an impending eye movement might be too late for some perceptual functions [4], and referencing the transfer to an earlier allocation of attention is an attractive concept.

However, three points in the Cavanagh *et al.* article [1] are problematic. First, some of the ideas regarding RFs are overly simple. The paper generally ignores the fact that points in visual space can be computed from population codes of relatively large RFs and do not necessarily require a huge array of small, retina-like RFs. The computationally intensive model in Figure 2B is therefore unnecessarily elaborate. Likewise, we believe it is important to keep in mind that RFs in FEF and LIP have diameters of the order of $\sim 10\text{--}20^\circ$ [e.g. 5, 6] at eccentricities often used in human psychophysical experiments ($\sim 10^\circ$). The relevance of such experiments to remapping is questionable unless researchers ensure that stimuli are separated by at least the RF diameter distance. Otherwise all stimuli might be contained within a single RF before and after an eye movement, rendering remapping unnecessary.

Second, the authors do not provide criteria to help distinguish between the applicability of the presented models. One possible remedy is to provide a provisional, neuron-based account of attentional pointers. Would the authors expect to see representations of attentional pointers in the activity of single neurons within a brain area, in local microcircuits, or in correlated activity as a broader

representation across areas? Such basic information would go a long way towards establishing attentional pointers as a testable hypothesis.

Lastly, it seems unlikely that remapping is feature-independent. Neuronal responses in areas that remap, such as LIP, encode stimulus properties in addition to location [7–9, for review, see 10]. It is hard to imagine that remapped signals are stripped of this tuning to become mere pointers. Specific experiments have begun to test this idea and find that at least some tuning is maintained during remapping [see Subramanian *et al.* (2009) Shape selectivity during remapping in macaque lateral intraparietal area. 2009 Society for Neuroscience annual meeting, abstract # 758.8].

Similar to Cavanagh *et al.* [1], we believe that research on remapping can profit from an integration of research on spatial attention and visuomotor orienting, which have remained largely segregated. We take the article by Cavanagh *et al.* as a welcome invitation to elucidate the neuronal mechanisms of remapping in relation to attention.

References

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