Attention Pointers: Response to Mayo and Sommer

Patrick Cavanagh^{1,2}, Amelia R. Hunt³, Arash Afraz⁴ and Martin Rolfs⁵

¹ Laboratoire Psychologie de la Perception, Université Paris Descartes, 45 rue des Saints Pères, 75006 Paris, France

² Vision Sciences Laboratory, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA

³ School of Psychology, William Guild Building, University of Aberdeen, Aberdeen, AB24 2UB, UK

⁴McGovern Institute for Brain Research, Massachusetts Institute of Technology, 43 Vassar Street, Cambridge, MA 02139, USA

⁵ Department of Psychology, New York University, 6 Washington Place, New York, NY 10003, USA

Mayo and Sommer [1] raise several interesting questions about our opinion article [2]. First, they propose that the receptive field (RF) sizes in saccade control areas are too large to support the localization of attentional benefits seen in behavioral studies. Clearly the RF sizes in these areas are large, but attentional resolution is correspondingly extremely crude [3]. However, the RF sizes in frontal eye fields (FEF) and lateral intraparietal (LIP) area are perhaps twice as large as the corresponding 'attentional field' at the same eccentricity. On this point we agree with Mayo and Sommer that localization cannot be a function of individual RFs but of populations. Saccade targeting is more accurate than the size of individual fields in saccade control areas [4] and more similar to the size of attentional selection areas. We did depict the models of remapping (e.g. [5]) as relying on individual cells but that was an oversimplification. Clearly, saccade and attention targets must be indexed by a profile of activity across many responding units and this entire profile would be subject to remapping. Even if a stimulus would remain within the RF of a single cell after a saccade, the population of responding cells would shift.

Second, Mayo and Sommer ask if there is activity that is specific to the attention pointer either in single neurons, local microcircuits or more global networks. We assumed that the function of the attention pointer was inherent in the well-documented properties of saccade control areas that specify the target location and provide, through downward projections, attentional benefits at the corresponding locations (review in [6]), instantiating the essential functions of spatial attention. In this view, the attentional benefits are an obligatory consequence of activity in the saccade areas, not an optional related activity. When a saccade is programmed, the activity peaks for current targets are remapped to compensate for their upcoming shift in retinal locations. As the activity peaks of attended targets shift to new locations, their attentional benefits shift with them. Here 'attended' means nothing more or less than the object or features at the retinal location corresponding to an activity peak. We argued, in particular, that remapping is not a RF shift (Box 1) but an anticipatory response. This does raise the question of how the downward projections arise and how accurately they target neurons in earlier cortices. Nevertheless, our labeling of this localized performance advantage as an 'attentional pointer' only specifies that the activity ident-

Box 1. Attention-driven RF shifts vs. remapping

Mayo and Sommer point out that the centers of large RFs at intermediate levels do shift toward an attentional focus (e.g. [7]). Saccade targets clearly set up an attentional focus, so Mayo and Sommer's point naturally raises the possibility that the remapping shifts are related to these attention-driven shifts (see also [8]). However, we argue that these attention-driven effects cannot generate RF shifts of the magnitude required for remapping; they are much too small. A RF must necessarily shift 100% of the saccade magnitude to match the remapping results whereas attention-driven RF shifts are at best 30% on average of the separation from target to attentional focus [7] and never reach the 50 to 90 deg displacements that saccades easily do. Moreover, changes in RFs in middle temporal area (MT) and V4 occur around the focus of attention [7], as well as around a saccade target [9]; the important point is that eye movements are not necessary for these RF modulations to be observed. By contrast, remapping is only seen when an eye movement is executed, and does not occur for attention shifts [10], indicating it serves a separate function. The changes in MT and V4 have been linked to enhancement of processing at attended locations; remapping maintains that processing enhancement at spatially appropriate locations by shifting activity peaks to the new retinotopic location of attended locations when the eyes move.

ifies the location of the target to which performance benefits are provided.

Finally, along with Mayo and Sommer, we feel it is crucial to determine to what extent the individual neurons in saccade centers have featural specificity independently of task relevance and to what extent the performance benefits from downward projections can be tuned to target features. This is an ongoing exploration and although we claimed it would be more plausible that remapping of activity did not convey feature information, the final answer will emerge from ongoing work in our lab and elsewhere.

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Corresponding author: Cavanagh, P. (patrick.cavanagh@parisdescartes.fr).

Update

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