From a Different Point of View: Extrastriate Cortex Integrates Information Across Saccades. Focus on "Remapping in Human Visual Cortex"

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An enduring question in cognitive neuroscience regards the mechanisms by which the brain constructs a stable representation of the external world despite constant movement of the observer—the mechanisms of "spatial constancy". Evidence from single-neuron recording shows that visually responsive neurons, even in high-level visual areas, typically have receptive fields that are retinotopic (linked to the retina) and thus encode the ever-changing retinal image rather than a stable, spatiotopic, view of the world. However, some neurons in dorsal stream visuomotor areas show a phenomenon known as "remapping" that may provide a substrate for at least some forms of spatial constancy. In addition to responding to visible stimuli in their receptive field, these neurons also reflect the memory of a salient event that occurred outside of their receptive field if the spatial location of that event (itself no longer visible) enters their receptive field by virtue of an eye movement (Duhamel et al. 1992; Gottlieb et al. 1998; Umeno and Goldberg 1997). In other words, neurons have a form of spatially accurate memory that could link information about a constant object or location that is gleaned in successive fixations. In their manuscript in this issue of the *Journal of Neurophysiology* (p. 1738–1755), Merriam et al. show that a phenomenon very similar to remapping occurs in extrastriate cortical areas in humans, bolstering the hypothesis that remapping is important for perceptual constancy and visual integration across eye movements.

For their fMRI study Merriam et al. ingeniously adapted behavioral tasks previously used in single-neuron recordings in monkeys (Merriam 2007). Each trial started when subjects fixated an eccentric fixation point and observed a briefly flashed visual stimulus. After the stimulus disappeared, the subjects made a rapid eye movement (saccade) a different fixation point. This saccade changed the location of the recent (but now extinguished) visual flash relative to the retina. The authors set up the experiment so that the initial and new retinotopic locations fell in opposite hemifields. For instance, in one condition subjects initially fixated 8° to the left and the stimulus flashed in the right visual field. The subjects then made a large saccade bringing the eye 8° to the right, which brought the location of the recent flash into the left hemifield. Even though the flash was no longer visible at the time of the saccade, extrastriate visual areas representing the postsaccadic hemifield of the flash (the left hemifield) showed significant activation, as if they remapped the memory of the visual stimulus relative to the new eye position. Careful statistical analyses showed that these remapping responses were above and beyond those expected from control conditions in which the stimulus or saccade were presented alone. Remapped responses

were strongest in area hV4 (human area V4) and progressively weaker in areas V3a, V3, V2, and V1, declining in rough proportion with the position of areas in the visual hierarchy.

By its very nature remapping is a visuomotor, not a purely visual phenomenon. To accurately infer the postsaccadic location of a past event, a memory trace of initial stimulus location must be combined with information about the metrics of the intervening movement. Perhaps not surprisingly therefore remapping was originally described in dorsal stream visuomotor areas including the lateral intraparietal area (LIP), the frontal eye field (FEF), and the superior colliculus (SC), which carry both retinotopic visual memory signals and information about saccade metrics. The finding that remapped responses are also found in extrastriate areas implies that these areas receive some form of top-down information—either information about saccade metrics that enables a local computation of the remapped response or the final result of a remapping computation that is initially carried out in the dorsal stream.

Psychophysical evidence suggests that remapping is important for spatial localization. For instance, it is known that human subjects make systematic errors in reporting the location of remembered visual events in a time window of 100 ms before to 100 ms after the saccade (Ross et al. 1997). This period of spatial uncertainty corresponds well with a period of ambiguity in the remapped response itself: in areas LIP and V3A in the monkey, remapping begins slightly before the eye movement so that around the time of the saccade neurons with receptive fields at both the initial and remapped stimulus locations are active simultaneously (Kusunoki and Goldberg 2003; Nakamura and Colby 2002). Both spatial and temporal characteristics of this ambiguity in neural responses correspond with the ambiguity in the perceptual report, consistent with the possibility that perceptual localization relies on remapping.

Perhaps more directly relevant to the experiment of Merriam et al., remapping may also contribute to the integration of information about visual features (such as form or motion) across saccades (Cox et al., 2005; Melcher and Morrone 2003), and such, trans-saccadic integration may occur to a different extent for different levels of visual analysis (Melcher 2005). Melcher used a clever visual adaptation protocol, in which he showed subjects an adapting and a test stimulus at a constant spatial location. In some trials, subjects maintained fixation so that the adapting and test stimuli also stimulated the same retinal location; in other trials, however, subjects made a saccade between the adaptation and test period so that the retinal locations of the two stimuli differed. Whereas contrast adaptation was entirely retinotopic (was fully abolished by the

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change in retinotopic position), face adaptation was entirely spatiotopic and was unaffected by dissonance in retinotopic position. Adaptation for intermediate properties such as tilt and form was partially spatiotopic and partially retinotopic. Thus the spatially accurate integration of information across saccades seems to be a graded property, carrying progressively more weight at higher stages of visual analysis. This appears consistent with the finding of Merriam et al. that remapping is progressively stronger along the hierarchy of visual cortical areas. The challenge now is to provide direct evidence, using simultaneous physiological and psychophysical measurements in the same subject, that remapping in extrastriate cortex is indeed functionally related to the integration of visual information from a constant object across eye movements.

REFERENCES

Cox DD, Meier P, Oertelt N, DiCarlo JJ. "Breaking" position-invariant object recognition. *Nat Neurosci* 8: 1145–1147, 2005.

Duhamel J-R, Colby CL, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90–92, 1992.

Gottlieb J, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. *Nature* 391: 481–484, 1998.

Kusunoki M, Goldberg ME. The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *J Neurophysiol* 89: 1519–1527, 2003.

Melcher D. Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Curr Biol* 15: 1745–1748, 2005.

Melcher D, Morrone MC. Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nat Neurosci* 6: 877–881, 2003.

Merriam EP Remapping in human visual cortex. *J Neurophysiol* 97: 1738–1755, 2006.

Nakamura K, Colby CL. Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proc Natl Acad Sci USA* 99: 4026–4031, 2002.

Ross J, Morrone MC, Burr DC. Compression of visual space before saccades. *Nature* 386: 598–601, 1997.

Umeno MM, Goldberg ME. Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J Neurophysiol* 78: 1373–1383, 1997.