We favor another of the authors' ideas: that these axons provide an anticonvulsant influence when seizures threaten. A copious literature documents the tendency of many axon types to fire ectopically before (interictally) and during seizures[1,4,5,7,8]. Axon collaterals of excitatory neurons might help to spread seizures, but they also activate interneurons that trigger strong, phasic inhibition[5]. Spiking patterns associated with seizures are similar to those that induce persistent firing in Htr5b interneurons[2]. If the axons of some interneurons fire persistently and autonomously, then they could provide tonic inhibition that helps to ameliorate or prevent seizures. Sorting through the fascinating possibilities will require challenging experiments *in vivo*.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

1. Pinault, D. *Brain Res. Brain Res. Rev.* **21**, 42–92 (1995).
2. Sheffield, M.E., Best, T.K., Mensh, B.D., Kath, W.L. & Spruston, N. *Nat. Neurosci.* **14**, 200–207 (2011).
3. Moore, J.W., Stockbridge, N. & Westerfield, M. *J. Physiol.* **336**, 301–311 (1983).
4. Gutnick, M.J. & Prince, D.A. *Science* **176**, 424–426 (1972).
5. Noebels, J.L. & Prince, D.A. *J. Neurophysiol.* **41**, 1267–1281 (1978).
6. Papatheodoropoulos, C. *Neuroscience* **157**, 495–501 (2008).
7. Traub, R.D., Bibbig, R., Piechotta, A., Draguhn, R. & Schmitz, D. *J. Neurophysiol.* **85**, 1246–1256 (2001).
8. Keros, S. & Hablitz, J.J. *Neuroscience* **131**, 833–842 (2005).
9. Connors, B.W., Ransom, B.R., Kunis, D.M. & Gutnick, M.J. *Science* **216**, 1341–1343 (1982).
10. Lai, H.C. & Jan, L.Y. *Nat. Rev. Neurosci.* **7**, 548–562 (2006).
11. Shu, Y., Yu, Y., Yang, J. & McCormick, D.A. *Proc. Natl. Acad. Sci. USA* **104**, 11453–11458 (2007).
12. Kapoor, R., Smith, K.J., Felts, P.A. & Davies, M. *Brain Res.* **611**, 165–169 (1993).
13. Hounsgaard, J. & Nicholson, C. *J. Physiol.* **340**, 359–388 (1983).
14. Kovalsky, Y., Amir, R. & Devor, M. *J. Neurophysiol.* **102**, 1430–1442 (2009).
15. Bacci, A. & Huguenard, J.R. *Neuron* **49**, 119–130 (2006).

Attention points to the future

Richard J Krauzlis & Samuel U Nummela

Our perception of the visual world is stable despite saccade-caused retinal input shifts. A new behavioral study shows that this stability may be achieved by predictively remapping attention before eye movements begin.

If you move one of your eyes by (gently!) poking it with your finger, the entire visual world appears to move. But if you move the eye by making saccadic eye movements, those rapid flicks of the eye that direct your view from point to point—as you do, for example, while reading this sentence—the world remains stable. The difference lies in the ability of our nervous system to use internal signals to compensate for the sensory consequences of our own movements[1,2]. This is done partly by suppressing the visual consequences of the otherwise disruptive image blur that is caused by saccadic eye movements. It is also done by taking into account the displacement of the visual images caused by eye movements, so that the visual world appears stable, even though the retinal images shift again and again. A study in this issue of *Nature Neuroscience*[3] provides new insight into this classic problem in systems neuroscience.

Rolfs and colleagues[3] used a cleverly designed behavioral paradigm to test the functional consequences of saccade-related changes in visual processing. Human subjects are presented with a hexagonal array of six stimuli, and are asked to do two things. First, they are instructed to make a sequence of two saccades toward particular stimuli in the array—for example, a rightward saccade followed by a saccade upward and leftward. Second, they are asked to judge whether an oriented 'probe'

Richard J. Krauzlis and Samuel U. Nummela are in the Systems Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, California, USA.
e-mail: rich@salk.edu

stimulus, briefly presented at one of the six locations, is tilted to the right or the left. A key feature of the experimental approach is that the stimuli at the six locations are not static, but consist of a rapidly alternating stream of stimuli and masks, with the single probe stimulus mixed in. The upshot of this arrangement is that it can measure changes in visual sensitivity (how well the probe is detected amongst the masking stimuli), as well as the time course of these changes, just as the subject is about to begin the sequence of two saccades.

Discrimination performance is not equivalent across all locations but is strongly influenced by the planned saccades. It is well established that saccades are preceded by a shift of attention[4–6], and, in keeping with these previous studies, subjects are better at the hexagonal array task when the probe is located where the first saccade is about to land. However, the new finding of this study is that discrimination performance is also improved at the location targeted by the second saccade—and this improvement is evident even before the start of the first saccade. Thus, attention remaps to the retinotopic location of the second target, but, crucially, because this happens in retinotopic rather than world coordinates, and before the first saccade, the benefit is conferred on a stimulus that will not be the target of either the first or second saccade (**Fig. 1**).

This finding suggests that the allocation of attention is predictively remapped before saccades, and, in several control experiments, Rolfs *et al.*[3] rule out several less interesting interpretations. For example, it could be the case that attention is not remapped, but simply spread in the direction of the upcoming saccades. This possibility is ruled out by the finding that performance did not improve at every location in the direction of the saccade, but instead the benefit was specific to the remapped location. More control experiments help rule out the possibility that the effects are due to a purposeful strategy by the subjects, as well as show that the phenomenon also applies to foveal locations, which is especially important because the fovea is one of the defining specializations of the primate visual-motor system. Together, these findings provide convincing evidence for the predictive remapping of attention: the benefit of attention is present for future, as well as current, target locations.

A backdrop to these new results is the phenomenon of shifting receptive fields by visual neurons in various areas of the cerebral cortex and the idea that these shifting receptive fields are part of the mechanism for maintaining visual stability[2,7]. The classic finding is that the receptivity of some visual neurons changes around the time of saccades, such that they are excited by stimuli that are not now in their receptive field but that will fall in their receptive fields once the impending saccade is completed[8] (**Fig. 1a**). In effect, the neurons seem to 'sneak a peak' at the upcoming receptive field stimulus, before the saccade. By shifting their receptive fields, these neurons may provide a bridge between the pre- and post-saccadic representations of the visual world.

This property has been described for neurons in parietal and frontal cortex[8–10], in

superior colliculus[11] and also, in somewhat diminished form, in several areas of visual cortex[12,13]. Shifting receptive fields are often discussed as part of the mechanism for maintaining perceptual stability of the world, but the details of the phenomenon raise some doubts about this and suggest an alternate interpretation. In particular, the change in visual receptivity around the time of saccades does not occur equally for all stimuli, but occurs mostly for stimuli that are actively attended by the subject[14]. Thus, if shifting receptive fields are part of a neural mechanisms for maintaining visual stimuli, it is likely a mechanism for tracking the objects of your attention, not the full content of your visual environment. The idea of 'shifting receptive fields' succinctly captures the observed phenomenology, but for reasons delineated elsewhere[15], it also implies a mechanism that seems implausible. Is the visual system really wired up so that individual neurons can transiently shift their receptivity to an entirely new set of retinotopic inputs, depending on the direction and amplitude of the upcoming eye movement? The costs of wiring up such a pan-connected system would seem prohibitive.

Instead, these peri-saccadic changes in receptivity may be more accurately viewed as a 'transfer of activation', from the set of neurons involved in processing the attended objects before the saccade to the set of neurons needed to process the same objects once the saccade is completed[15]. This transfer of activity presumably involves a prediction about which neurons should be recruited for this transfer of activity, but the presence of a corollary discharge signal for eye movements provides a potentially robust basis for learning and implementing these predictions.

The results from Rolfs et al.[3] fit very nicely into this context. Their finding that attention predictively remaps before saccades is what one might expect if the nervous system has learned to transfer activity from the set of neurons now involved in processing the attended object to those that will be needed in the future, after the intervening saccades are completed (**Fig. 1b**). However, one odd aspect of the findings is that the timing of the putative transfer of activation is not particularly precise. The authors' conclusions rest on finding improved discrimination at the future location of the second target, even before the first saccade occurs, but this means that an irrelevant location (the 'remapped location') has been erroneously highlighted
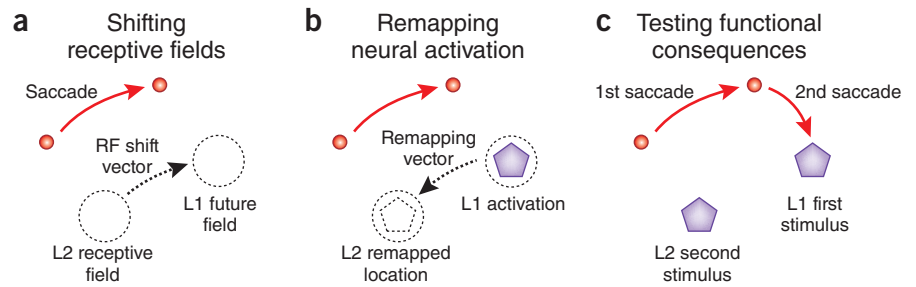
Figure 1 Testing the functional consequences of pre-saccadic remapping. Pre-saccadic remapping can be described either as shifting receptive fields (RFs) or the remapping of neural activation. (**a**) Shifting receptive fields. Just before a saccade, cells with a classical RF at a particular location in space, L2, become receptive to stimulation at the 'future field' location, L1, which is shifted away from the classical RF in the same direction as the saccade vector (RF shift vector). (**b**) Remapping neural activation. Because the target sweeps across the retina in the direction opposite to the saccade, the expected retinal location of the target after the saccade is in the direction opposite to the saccade. Neural activation therefore also remaps in the direction opposite to the saccade. (**c**) To test the functional consequences of this remapping, Rolfs et al.[3] had subjects make a sequence of two saccades and measured the remapping of attention for an attended peripheral stimulus (the second saccade target, L1). They found evidence of remapping even before the first saccade, which corresponds to a location (here, L2) that is not the target of either the first or second saccade. Modified from ref. 3.

for the 100 or so milliseconds until the eye moves. During this interval, subjects seem to pay extra attention to a frankly irrelevant part of the display (**Fig. 1c**).

This apparent discrepancy may be related to a limitation of the underlying mechanisms that introduce a brief window of vulnerability into our ability to localize and process visual stimuli with each saccade—perhaps the biology of neural signal transfer puts a speed limit on the transfer of activation. For example, the early deployment of attention to the irrelevant location before the saccade may be the cost incurred to guarantee that attention is fully deployed at the relevant location by the end of the saccade. One of the main unanswered questions is whether these same types of mechanisms are involved in the stable perception of visual objects. Rolfs et al.[3] show that predictive remapping of attention can be used to keep track of relevant locations across saccadic eye movements, but they leave open the question of whether similar remapping can keep track of object identity. The problem faced by the nervous system in keeping track of visual objects is quite profound because the set of visual neurons that encode the features of an object of interest (for example, its color and shape) can change completely with each saccade. Pooling the signals from the relevant subset of feature-sensitive neurons within each cortical visual area could, in principle, also be achieved by a transfer of activation for each

saccade, so that the identity of the visual object is maintained.

Testing this possible mechanism for tracking object identity will not be simple, but this line of work shows that the interaction between vision and eye movements provides a special opportunity to answer one of the principal riddles in visual neuroscience.

1. Sommer, M.A. & Wurtz, R.H. *Annu. Rev. Neurosci.* **31**, 317–338 (2008).
2. Wurtz, R.H. *Vision Res.* **48**, 2070–2089 (2008).
3. Rolfs, M., Jonikaitis, D., Deubel, H. & Cavanagh, P. *Nat. Neurosci.* **14**, 252–256 (2011).
4. Hoffman, J.E. & Subramaniam, B. *Percept. Psychophys.* **57**, 787–795 (1995).
5. Kowler, E., Anderson, E., Dosher, B. & Blaser, E. *Vision Res.* **35**, 1897–1916 (1995).
6. Deubel, H. & Schneider, W.X. *Vision Res.* **36**, 1827–1837 (1996).
7. Colby, C.L. & Goldberg, M.E. *Annu. Rev. Neurosci.* **22**, 319–349 (1999).
8. Duhamel, J.-R., Colby, C.L. & Goldberg, M.E. *Science* **255**, 90–92 (1992).
9. Umeno, M.M. & Goldberg, M.E. *J. Neurophysiol.* **78**, 1373–1383 (1997).
10. Kusunoki, M. & Goldberg, M.E. *J. Neurophysiol.* **89**, 1519–1527 (2003).
11. Walker, M.F., Fitzgibbon, E.J. & Goldberg, M.E. *J. Neurophysiol.* **73**, 1988–2003 (1995).
12. Nakamura, K. & Colby, C.L. *Proc. Natl. Acad. Sci. USA* **99**, 4026–4031 (2002).
13. Tolias, A.S. *et al. Neuron* **29**, 757–767 (2001).
14. Gottlieb, J.P., Kusunoki, M. & Goldberg, M.E. *Nature* **391**, 481–484 (1998).
15. Cavanagh, P., Hunt, A.R., Afraz, A. & Rolfs, M. *Trends Cogn. Sci.* **14**, 147–153 (2010).