

subunit NR2B while NR2B is in a transport vesicle and directs NR2B to the postsynaptic density. Schnapp argues that kinesin adaptors, by serving as scaffolds, can target the signaling complexes that they transport to appropriate, highly localized membrane destinations where their signaling functions are required. In this light, several properties of GRIP1 are likely to work in concert: its ability to bind EphB2 cargo, its ability to link this cargo to a kinesin and then steer the kinesin to dendrites, and

finally, the ability to scaffold the EphB2 cargo at an appropriate membrane destination. The Hoogenraad *et al.* study suggests that GRIP1's integration of these functions underlies a fundamental step in dendritic arborization.

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Distortions of time during rapid eye movements

David M Eagleman

Illusions of spatial vision can occur during rapid eye movements known as saccades. A new report shows that temporal judgments are also distorted around the time of saccades, suggesting that the neural representations of time and space may be linked.

Each second of your waking life, your eyes dash around in rapid, ballistic eye movements called saccades. As a result, your visual stream is like that of a hand-held video recorder held by a drunkard. Yet the visual world appears to remain stable. This stability is thought to be related to several types of spatial distortion that occur around the time of saccades: object locations can be spatially offset in the direction of the saccade target^{1,2}, objects parallel to the path of the saccade appear squashed³ and geometric relationships between objects can be distorted⁴. But what happens to time perception during a saccade is largely unknown. In this issue, Morrone *et al.* demonstrate that perisaccadic time judgments, like spatial judgments, can be subject to strange illusions⁵.

This new finding is important because although vision is typically thought of as a spatial phenomenon, its construction requires the brain to deal cleverly with time as well. To prove this, here's a quick party trick to lay bare the mysteries of time during a saccade. Look at your own eyes in a mirror and move your eyes back and forth so that you are looking at your left eye, then at your right eye, and so on. When your eyes shift from one position to the other,

they can take some tens of milliseconds in their ballistic flight. But here's the puzzle: you never see your own eyes move. What happens to the gaps in time while your eyes are moving?

This party trick alone should have spurred perisaccadic time research, but there are few examples in the literature. Saccadic suppression begins even before the eyes begin to move, and lasts well after the eyes land^{6,7}. Moreover, sometimes when you make a saccade to a clock on the wall, the second hand seems to stick for just a moment too long before resuming its regular pace. It has been speculated that this 'stopped clock' illusion results from the saccadic time gap being retrospectively filled by the scene the eye lands upon⁸. Aside from these reports, the study of time remains generally untapped⁹.

Broadcasting from this largely uncharted territory, Morrone *et al.* now report that duration judgments are compressed during sac-

ades⁵ (**Fig. 1**). Subjects compared two time durations: the first was presented close in time to a saccade, whereas the second was presented while the eyes were still. Surprisingly, the perisaccadic durations were underestimated by about a factor of two. In other words, a 100-ms duration around the time of a saccade would be judged equivalent to a ~50-ms duration presented later. Moreover, the precision of perisaccadic judgments improved when the duration was perceptually compressed. This duration compression effect did not occur with blinks; it was specific to saccades. The range in which the temporal compression was observed—both before and after a saccade—is roughly the same range in which spatial compression is found^{3,10}, suggesting the possibility of a common mechanism for time and space distortions.

Does this finding mean that subjective time has been compressed by a factor of two dur-

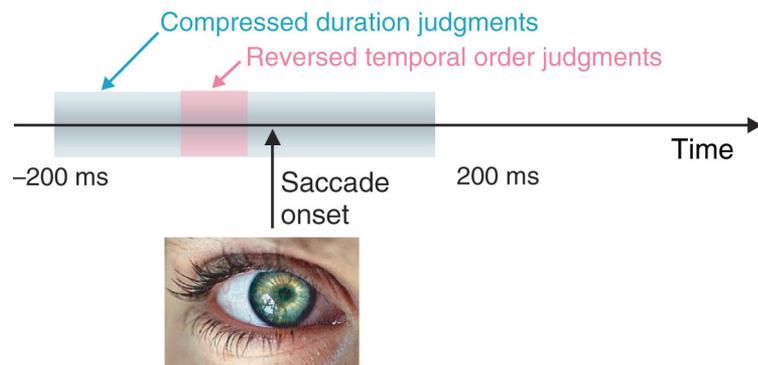


Figure 1 Two illusions of subjective time around the time of a saccade. Judgments of the duration between two targets are compressed around the onset time of a saccadic eye movement (blue). In a smaller window, temporal order judgments can become reversed when the two targets appear close in time to each other (red)⁵.

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ing the saccade⁵? One must be cautious in phrasing these matters, because the duration compression does not occur with auditory clicks—only with flashes. Therefore, it is not subjective time in general that is compressed; instead, only duration judgments about visual stimuli are modulated.

What might explain this duration compression? A good deal of excitement has been generated in the last decade about neurons found in lateral intraparietal area (LIP), superior colliculus and extrastriate cortex that dynamically remap their receptive fields around the time of a saccade¹¹. Some of these neurons show a receptive field shift that is anticipatory, as though they are predictively forming a view of the scene where the eyes are about to land. It has been suggested that this remapping may be directly related to perisaccadic spatial distortions¹². Following in that spirit, Morrone *et al.* suggest that the duration compressions, too, may result from the actions of dynamically remapping receptive fields, especially since LIP neurons participate in duration judgments¹³. Future neurophysiology experiments might be able to examine duration encoding during saccades to directly address this hypothesis.

Although the story of receptive field remapping starts off simply, it quickly becomes thorny. The remapping of LIP neurons is spread widely in time around a saccade: about one-third of the neurons change their coding predictively, while the remainder remap during or after the

saccade, with a spectrum of timings in between. This presses the question of how the remapping is temporally coordinated. It is unclear how such temporally spread signals could be related to an increase in precision found by Morrone *et al.* These considerations again remind us that the representation of time is as least as perplexing as the representation of space.

In addition to duration compressions, Morrone *et al.* report a second finding about time judgments during saccades, although its relationship to the first finding is currently unclear. Instead of duration judgments, they next asked subjects to make temporal order judgments: which of two targets appeared first? Within a small window before the saccade (−70 to −30 ms), they discovered a temporal inversion: two targets appearing within ~50 ms of each other were systematically perceived in the wrong order⁵ (Fig. 1). Subjects were not simply worse at making judgments in this range: the order judgments were actually reversed. As the authors acknowledge, a clean explanation is still missing for this result.

The Morrone *et al.* study may introduce more questions than answers. For example, although some evidence implicates LIP neurons in duration judgments¹³, no evidence yet implicates them in temporal order judgments. It may be that temporal order judgments are constructed retrospectively from differentially distorted duration judgments, but this assumption cannot be taken for granted and,

moreover, would not clarify the different time windows of the two effects (Fig. 1).

Time will be critical in the emerging story of vision as an active construction of the world around us. Previous suggestions that the brain constructs its evolving picture of the world by optimal integration across saccades¹⁴ will need to be revisited with these new timing discoveries in hand. Whatever the outcome, the new Morrone *et al.* findings bode well for a future in which neuroscience—like physics before it—attends to the relationship between time and space.

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Auditory cortex cheers the overture and listens through the finale

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Although we hear sounds throughout their duration, studies on anesthetized animals have suggested that auditory cortex neurons primarily detect changes in sound. New evidence in a report in *Nature* from awake animals is forcing us to reconsider this view.

In the visual system, some neurons habituate rapidly to a featureless blue sky but readily detect the appearance of a bird passing overhead. Likewise, many studies have reported that neurons in auditory cortex of anesthetized animals demonstrate brief bursts of spikes (called ‘phasic responses’) to acoustic onsets or transients, but show little or no

tonic activity during the remainder of the sound. It would seem to be a reasonable strategy on the part of the brain to devote more resources to marking changes in the sensory world than to monitoring the steady state: “Ho hum, there’s nothing new over here.” However, one must ask how it is that a viewer knows that the sky continues to be blue and featureless or that a listener knows that a tone continues to play. If auditory perception were derived solely from phasic responses, one would expect the perception of an unmodulated tone to fade to silence within milliseconds. In contrast, we know

that auditory percepts persist throughout sounds lasting seconds or even minutes.

A report from Wang and colleagues¹ in a recent issue of *Nature* seems to resolve this conundrum. The report contains three key observations. First, unlike the situation in anesthetized animals, many neurons in the auditory cortex of awake marmosets responded throughout the duration of sounds, even for pure-tone stimuli that typically produce highly phasic responses under anesthesia. This observation provides a possible explanation for the persistence of auditory percepts. Second, the tonic responses were more selective for par-

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