

Correspondences

When your eyes see more than you do

Abtine Tavassoli  
and Dario L. Ringach

Visual information is used by the brain to construct a conscious experience of the visual world and to guide motor actions [1]. Here we report a study of how eye movements and perception relate to each other. We compared the ability of human observers to perceive image motion with the reliability of their eyes to track the motion of a target [2–4], the goal being to test whether both motor and sensory processes are based on the same set of signals and limited by a shared source of noise [2,4]. We found that the oculomotor system can detect fluctuations in the velocity of a moving target better than the observer. Surprisingly, in some conditions, eye movements reliably respond to the velocity fluctuations of a moving target that are otherwise perceptually invisible to the subjects. The implication is that visual motion signals exist in the brain that can be used to guide motor actions without evoking a perceptual outcome nor being accessible to conscious scrutiny.

Our task involved the visual tracking of a high-contrast Gabor target (Figure 1A, top) moving horizontally at a speed of 4° per second onto which we introduced a brief velocity perturbation half-way through the 3 second trial. The perturbation consisted of a single cycle of sinusoidal velocity profile that could be either peak-first or peak-last (Figure 1A, bottom) [5]. Subjects were instructed to visually track the motion of the target as closely as possible and to report, at the end of each trial, the type of velocity perturbation observed (peak-first or peak-last). We simultaneously recorded behavioral responses and eye movements for a range of perturbation magnitudes.

Psychometric curves were calculated as the probability of a correct discrimination at different perturbation magnitudes (Figure 1C, gray curves). Oculometric curves were obtained as the output of a simple

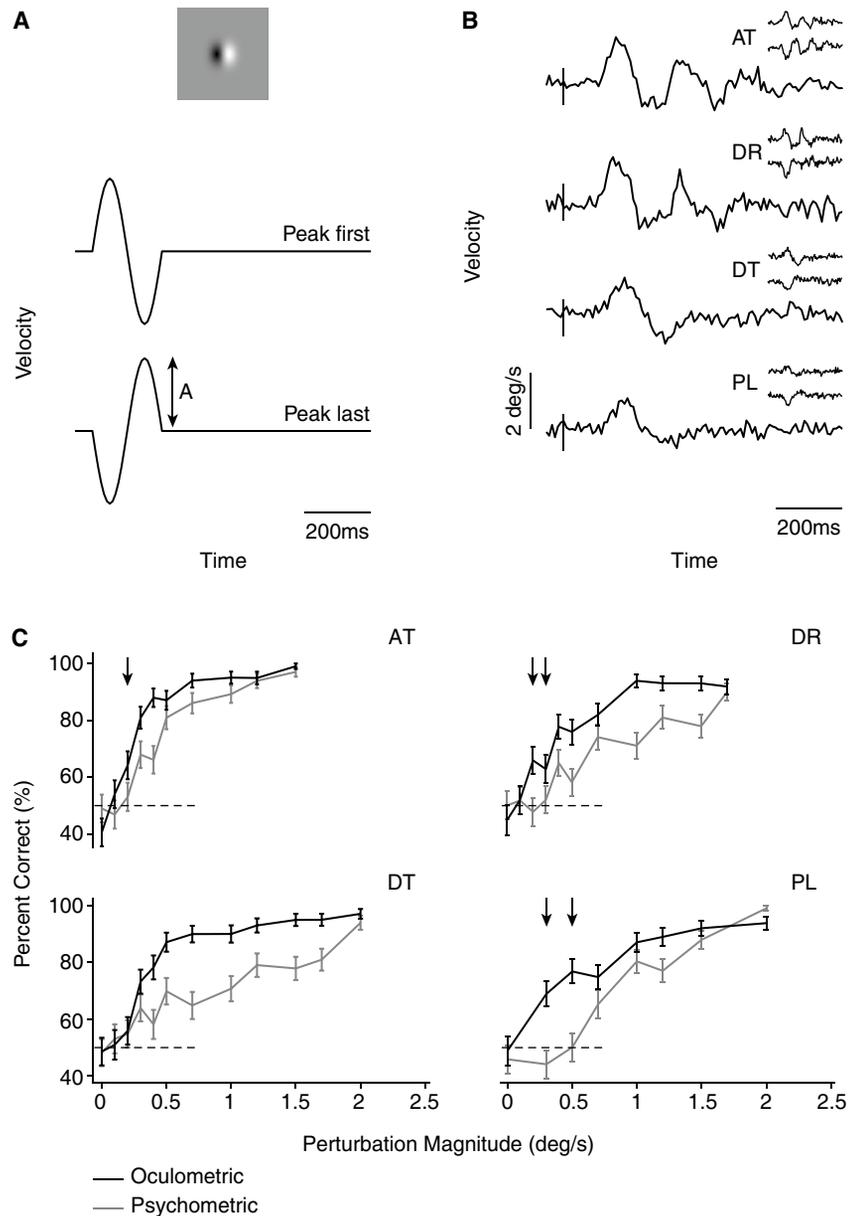


Figure 1. Experimental design and eye velocity responses.

(A) *Top*. A small Gabor target jumps horizontally to the left or right and moves in the opposite direction with a mean velocity of 4°/s. *Bottom*. A single-cycle sinusoidal perturbation of amplitude  $A$  is introduced during the tracking of the Gabor target, as previously done by Churchland and Lisberger (2002). We define the *magnitude* of the perturbation as the standard deviation of the perturbation signal, which equals the amplitude divided by the square root of two. (B) Mean responses were computed as the difference between the mean response to peak-first and peak-last. This is the  $f(t) - l(t)$  signal used in the classifier. The waveforms at the inset for each show the shape of the individual curves,  $f(t)$  and  $l(t)$ . (C) Comparison of oculometric and psychometric performance in the motion discrimination task. The black traces show the oculometric performance of 4 subjects. The gray traces show their psychometric performance. The error bars indicate the bootstrap estimates of the standard deviation at the different perturbation magnitudes. The horizontal dotted lines represent a chance performance of 50%. The arrows point to perturbation amplitudes for which psychophysical performance remained at chance levels while oculometric performance was clearly above chance. In other words, the eyes were able to respond to the velocity perturbations whereas the observer could not see them at all.

linear classifier operating on the horizontal eye velocity of an *individual* trial  $x(t)$  as follows. If  $\int [f(t) - l(t)] x(t) dt > 0$ , then the classifier decides the stimulus was peak-first; otherwise, it decides it was peak-last. Here,  $f(t)$  is the mean eye velocity in response to the peak-first condition, while  $l(t)$  is the mean response to the peak-last condition. These mean responses (or templates) were obtained for each subject from an *independent* set of experimental trials with perturbation amplitudes of  $2^\circ$  per second where the only task was to pursue the target (Figure 1B). Based on the temporal course of these responses, we chose the limits of integration in the classifier from 100 ms to 800 ms after the onset of the perturbation. The probability of correct responses derived from the classifier yields oculometric curves that can be directly compared to psychometric performance (Figure 1C, black curves). Because the classifier is not necessarily optimal, our method provides a lower bound on the amount of information contained in the eye movement traces. In other words, it is possible that there is more information in the eye velocity traces than we can actually extract using our linear decoding technique.

Oculometric performance was, nonetheless, noticeably better than psychometric performance over a large range of perturbation sizes (black above gray curves, Figure 1C). Surprisingly, for some small perturbation magnitudes, psychophysical performance remained at chance levels while oculometric performance was clearly above chance (Figure 1C, arrows). This means that, in some conditions, visual signals could drive eye movements without having any perceptual consequence.

The proportion of observer's errors were uncorrelated with the absolute value of the classifier signal (the absolute value of the integral in the equation above) (data not shown). This shows that perceptual errors were independent of the accuracy of pursuit eye movements. In other words, subjects do not appear to have a direct access to an efference copy signal of the motor command controlling pursuit eye movements that could be used to make perceptual judgments. One may wonder if the eye movements triggered by the perturbation in the

target velocity induce a subsequent retinal slip that could mask the perception of target motion. Control experiments, where the target is blanked right after the perturbation signal, rule this possibility out (see Supplemental Data available on-line with this paper).

Previous studies measured speed discrimination thresholds during pursuit eye movements and reported worse oculometric than perceptual performance during the initiation phase of pursuit, but similar performance during steady-state pursuit [3,4]. Kowler and McKee [3] observed that while sensory information regarding target velocity was available for perceptual discrimination it was not effectively used for pursuit during the initiation period. Gegenfurtner and colleagues [4] also found behavioral and eye movement responses to be uncorrelated from trial to trial. They suggested that the results could be explained with a common signal driving both eye movements and perception, both being corrupted at a later stage by independent noise sources.

Indeed, if the exact same pool of MT neurons are driving both perceptual judgments and smooth pursuit commands, one possible explanation for the results is the presence of larger amounts of noise and a more severe low-pass temporal filtering — a longer 'integration window' — in the path leading these signals to the generation of a conscious visual percept than in the path leading them to the generation of motor commands. It is also possible that a nonlinearity leading to perceptual judgments compresses motion signals of small amplitude, thereby generating higher thresholds for the psychometric curves. One must further consider the possibility that different sets of neurons within MT, with different signal-to-noise properties, support these two different uses of visual motion information. Our data cannot discriminate between these alternatives; the results, however, are in conflict with the notion that both motor and sensory processes are based on the same set of signals and limited by a shared source of noise [2].

Dissociations between visual perception and other types of eye movements, such as saccades and

vergence, have been reported. One example is a task where subjects must saccade to the first of two targets appearing in succession after a brief temporal delay, the saccadic system detects their temporal order better than the observers can apparently report [6]. Another example is the fact that vergence eye movements can be evoked by anti-correlated random dot patterns that otherwise evoke no changes in perceived depth [7].

Our study provides the first instance of such a dissociation between smooth pursuit and perceived image motion (both tasks thought to rely on the activity of neurons in area MT [8,9]), by showing that small perturbations in target velocity can be detected by the oculomotor system while being perceptually invisible to the observers. In a way, your eyes know more than you do.

#### Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)02063-6](http://www.cell.com/current-biology/supplemental/S0960-9822(09)02063-6)

#### Acknowledgements

This work was supported by National Eye Institute Grants EY-12816 and EY-18322.

#### References

1. Milner, A.D., and Goodale, M.A. (2008). Two visual systems re-viewed. *Neuropsychologia* 46, 774–785.
2. Osborne, L.C., Lisberger, S.G., and Bialek, W. (2005). A sensory source for motor variation. *Nature* 437, 412–416.
3. Kowler, E., and McKee, S.P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Res.* 27, 993–1015.
4. Gegenfurtner, K.R., Xing, D., Scott, B.H., and Hawken, M.J. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *J. Vis.* 3, 865–876.
5. Schwartz, J.D., and Lisberger, S.G. (1994). Initial tracking conditions modulate the gain of visuo-motor transmission for smooth pursuit eye movements in monkeys. *Vis. Neurosci.* 11, 411–424.
6. Leach, J.C., and Carpenter, R.H. (2001). Saccadic choice with asynchronous targets: evidence for independent randomisation. *Vision Res.* 41, 3437–3445.
7. Masson, G.S., Busettini, C., and Miles, F.A. (1997). Vergence eye movements in response to binocular disparity without depth perception. *Nature* 389, 283–286.
8. Newsome, W.T., Britten, K.H., and Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. *Nature* 341, 52–54.
9. Lisberger, S.G., and Movshon, J.A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *J. Neurosci.* 19, 2224–2246.

Departments of Neurobiology and Psychology, Jules Stein Eye Institute, David Geffen School of Medicine, University of California, Los Angeles, CA 90095, USA. E-mail: [dario@ucla.edu](mailto:dario@ucla.edu)