

## Journal Club

**Editor's Note:** These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see [http://www.jneurosci.org/misc/ifa\\_features.shtml](http://www.jneurosci.org/misc/ifa_features.shtml).

## Optimally Straight and Optimally Curved Saccades

Mark R. Harwood and James P. Herman

Department of Biology, City College of New York, City University of New York, New York, New York 10031

Review of Chen-Harris et al. (<http://www.jneurosci.org/cgi/content/full/28/11/2804>)

Your reading of this text is punctuated by brief episodes of effective blindness while executing point-to-point saccadic eye movements. We are unaware of these visual disruptions because each saccade lasts only a few tens of milliseconds. However, during many tasks we make two to three saccades per second and thus are effectively blind for 10% of that task time. The payoff for this drastic visual loss is the vastly superior acuity derived from the central 2° of maximal cone density of the retina. It is vital that saccades are kept both brief and accurate.

Speed and accuracy are often in competition: we can move a mouse pointer slowly to be more accurate, or faster and then correct errors. We have no such voluntary control over saccade speed: speeds are fixed for a given saccade size. This stereotypy, and the remarkably rapid, saturating firing rates of motoneurons during saccades, have suggested that saccades are as fast as possible within neuromuscular limits, and their speed is not modulated to increase accuracy. Instead, two independent mechanisms have been proposed to ensure accuracy. First, during a movement, because visual feedback takes too long, an internal feedback of the motor command indicates the progress of the eye and adjusts the duration of movement to terminate it when the appropriate end-

point is reached (Jürgens et al., 1981). Second, after a movement, accuracy is monitored and consistent unexpected errors between target and eye positions are reduced by recalibrating the system to match the amplitude of motor output to the intended amplitude of the saccade. Many observations show that these bottom-up mechanisms of neuromuscular limits, internal feedback, and adaptive control are sufficient to explain how speed and accuracy are maintained.

An alternative, optimization approach assumes that saccades, like other rapid movements, trade off speed and accuracy, but have a very narrow range of tolerable trade-offs outside of which the costs of saccadic inaccuracy (poorer acuity) and duration (disrupted vision) become prohibitive. We could make faster saccades, but these would be pointlessly inaccurate. Harris and Wolpert (1998) proposed a universal model for rapid movements in which speed/accuracy trade-offs result from signal-dependent noise on the motor command. Faster movements require faster neuronal firing rates (larger control signals), generating more signal-dependent noise, which increases endpoint variability; slower movements generate less endpoint variability, but are more time consuming. Minimizing explicit costs assigned to saccade duration and endpoint inaccuracy can explain saccade kinematics (Harris and Wolpert, 2006) with greater precision than current bottom-up models (Harwood et al., 1999). Unfortunately, one cannot prove that speed and accuracy are, in fact, optimized, because optimization and

bottom-up models produce similar behavior.

Optimization models can, however, more easily explain the straightness of slightly oblique saccades. This is surprisingly problematic for bottom-up saccade models (Becker and Jürgens, 1990), because the fixed speed and duration of horizontal and vertical saccades of a given amplitude predict strongly curved trajectories for slightly oblique movements (Fig. 1A). Contrary to the bottom-up concept of neuromuscular speed limits, the speeds of both horizontal and vertical components (produced by anatomically separated premotor burst generators) are slowed, or durations stretched, to give straight movements (Fig. 1B). Stretching not only straightens saccades, but also reduces the motor-command amplitude and, thus, the signal-dependent noise of each component. Turning the argument around, both motor commands must be reduced to avoid increasing endpoint variability when there are two potential noise sources. Optimizing a fixed speed/accuracy trade-off naturally produces vectorially coded, straight trajectories.

In their recent paper in *The Journal of Neuroscience*, Chen-Harris et al. (2008) extended the Harris and Wolpert (2006) model to include internal feedback, providing new evidence for optimization and demonstrating that bottom-up mechanisms can complement optimality explanations. Their model predicted that during cross-axis adaptation, in which a target is stepped vertically during a horizontal saccade (Fig. 1C), saccade trajectories should be curved late in the move-

Received April 24, 2008; revised June 9, 2008; accepted June 10, 2008.

Correspondence should be addressed to Mark R. Harwood, Department of Biology, City College of New York, City University of New York, Convent Avenue at 138th Street, New York, NY 10031. E-mail: mharwood@sci.cuny.edu.

DOI:10.1523/JNEUROSCI.1817-08.2008

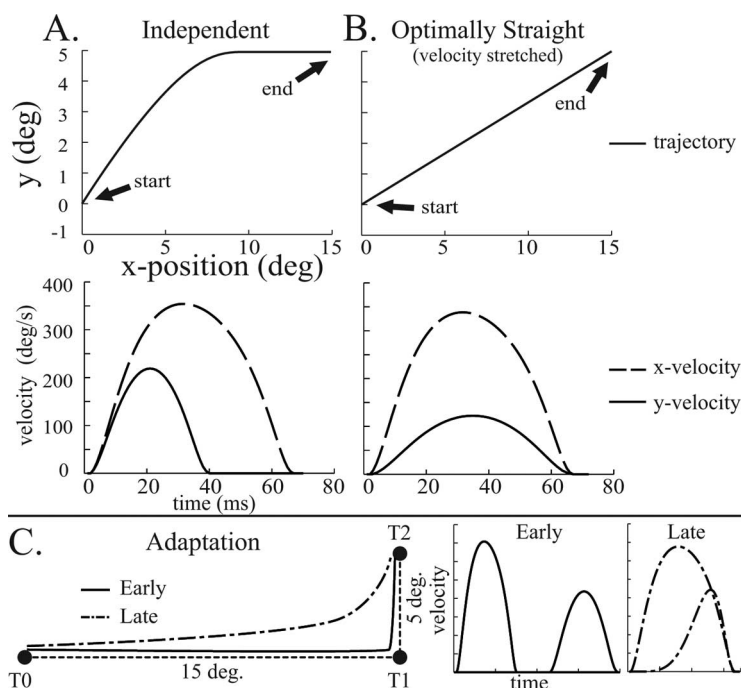
Copyright © 2008 Society for Neuroscience 0270-6474/08/287455-03\$15.00/0

ment. They found the predicted curvature, as well as intriguing parallels in the time courses of curvature and speed that may help unify disparate observations in the literature.

Chen-Harris et al. (2008) computed unadapted saccade trajectories that minimized costs related to postsaccadic inaccuracy, motor signal amplitude, and saccade duration. Optimization was performed recursively, with the motor command generator being updated continually by its predicted consequences (a “forward model,”  $FM_{eye}$ , producing a type of “dynamic motor error”). To predict the progress of the eye,  $FM_{eye}$  simply replicated the mechanics of the eye. This process [Chen-Harris et al. (2008), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/F2>)] generated realistic velocity shapes and straight saccades, and each cost was weighted to give typical durations for a given amplitude.

Next, the authors modeled the effects of cross-axis adaptation. When the eye lands below the target (because of an unseen upward target step during the saccade) (Fig. 1C), the brain may assign this error to  $FM_{eye}$  (because its purpose is to correct any deviations from the optimal trajectory, guiding the eye to its intended position). In this case,  $FM_{eye}$  would be updated to predict that a horizontal movement is actually aiming downward. This downward estimate drives an upward compensation of the trajectory [Chen-Harris et al. (2008), their Eqs. S5 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/DC1>) and 7 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/FD7>)]. Essentially, instead of simply deviating upward, the optimal trajectory curves increasingly upward (Fig. 1C). Although the authors call this curved saccade suboptimal because it does not go straight to the new position, it is optimal in speed and accuracy costs, given the modified  $FM_{eye}$ . If, instead, the controller that aims the saccade were adapted, upward deviation would be followed by downward curvature, whereas simply remapping the target or adapting  $FM_{eye}$  and controller equally would produce straight optimal paths.

Subjects showed clear upward curvature late in their saccades, supporting adaptation of  $FM_{eye}$  [Chen-Harris et al. (2008), their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/F3>)]. Before adaptation, 0–3° oblique saccades were, on average, straight. During adaptation, the whole trajectory adapted upward, but the final quarter had a signifi-



**Figure 1.** Straight oblique and curved adapted saccades. **A**, Independent horizontal and vertical 5 and 15° saccades have highly stereotyped velocity profiles for a given amplitude (bottom). If each component were summed, the resulting trajectory would be curved (top). **B**, Instead, each is stretched to the duration of a 16° unidirectional movement (bottom); the result is straight (top). This makes it difficult to argue that saccade speeds are determined by a motoneuronal or muscular limit; it seems that the speed-amplitude relationship is deliberately planned. **C**, Cross-axis adaptation of Chen-Harris et al. (2008). The eye fixes on the target at T0 (left), which steps to position T1 and then during the saccade steps 5° to T2. During early adaptation trials, the eye follows the target to T1 and shortly afterward makes a corrective saccade to T2; in later adaptation trials, the saccades curve upward toward T2. Corresponding velocity profiles are shown on the right (the larger peaks being horizontal components).

cantly steeper slope, steering the eye toward the new target. This steering could not have been visually driven because “catch trials,” in which the target was turned off early in the movement, had the same trajectory slopes as noncatch trials, and a control experiment with large random-direction target steps during each saccade showed no curvature. The fact that the entire trajectory changed suggests that the controller adapted along with  $FM_{eye}$ , but at a slower rate, leading to upward curvature.

Our main caveat is that a simpler bottom-up mechanism may explain the findings of Chen-Harris et al. (2008) without recourse to their model and its assumptions. Saccades curved only when subjects expected the target would move in a particular direction; blocks of catch trials alone quickly abolished the curvature. We conjecture that this expectation, by itself, could cause localized activation in the superior colliculus, the principal subcortical region for programming saccades, related to the change in the saccade goal. Sequential activation of collicular movement fields leads to curvature (Port and Wurtz, 2003). Thus, any predictive signal feeding into the superior colliculus

during the movement (i.e., soon after the burst of collicular activity that drives the eye toward the initial target location) might induce curvature, without necessarily requiring it to be either optimal or specifically an adaptive change in the  $FM_{eye}$ .

This sequential excitation argument is an extension of those invoked to explain saccade curvature when a distractor is presented during saccade preparation to another target (McSorley et al., 2006). We suggest that a predictive signal may have an effect similar to that of the sensory input of a suddenly appearing distractor. Hence, distractor and cross-axis adaptive curvature might share the same collicular origin, with the former driven by upstream visual input and the latter by predictive target information (either from upstream or as a feedback signal). Although Chen-Harris et al. (2008) model different types of target remapping, their remapping is complete by saccade onset and so cannot induce upward curvature during the saccade. Moreover, they model adapting trajectories with a fixed duration, which would automatically give rise to horizontal and vertical components terminating simultaneously; but this ig-

noses the partial flexibility that the saccade system possesses in this timing. No details were given of the criteria used to measure real saccade endpoints, so it is difficult to interpret how much curvature may have been related to component endpoints that were not synchronized.

The best evidence from the study by Chen-Harris et al. (2008) that the  $FM_{eye}$  was adapted comes from their other main finding: the astonishingly regular increase in saccade duration (without changes in amplitude) during blocks of trials, which was largely reset during brief interblock breaks [Chen-Harris et al. (2008), their Fig. 5 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/F5>)]. The same pattern occurred in control experiments, where targets stepped to the identical locations but never during saccades. Regardless of their cause, these duration increases show the operation of the compensatory internal feedback, because saccade amplitude was unaffected by duration and speed changes. The curvature (as judged by the difference between the slopes of the first and last quarter of the trajectory) showed the same time course, steadily increasing during each block and resetting between blocks [Chen-Harris et al. (2008), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/28/11/2804/F4>)], implying that the curvature was mediated by the same mechanism as the duration increases: the internal feedback ( $FM_{eye}$ ).

An interesting test of the model by Chen-Harris et al. (2008) would be to measure target localization during adaptation. Briefly flashed targets are mislocalized after saccade adaptation, suggesting the flash is referenced to the intended rather than the actual landing position (Bahcall and Kowler, 1999). Adapting the  $FM_{eye}$  causes discrepancies between estimated and actual eye positions. Thus, in the paradigm by Chen-Harris et al. (2008), mislocalization might increase in parallel with curvature during adaptation blocks (as the  $FM_{eye}$  adapts rapidly) and might decrease during breaks (as the  $FM_{eye}$  rapidly forgets).

In summary, the main strength of the paper by Chen-Harris et al. (2008) is in providing a strong computational framework within which to study saccade adaptation and control. It promotes the idea of predictive sensory error and efference copy as central to adaptation, emphasizing a faster online corrective mechanism as well as the traditional offline adaptation. It both proposes and, perhaps, downplays the importance of target prediction. By showing how speed and accuracy optimization can be implemented via internal feedback, it could suggest physiologically testable hypotheses. If combined with detailed bottom-up data and modeling (Goossens and van Opstal, 2006), optimization and bottom-up approaches may converge in a comprehensive model of the saccade system.

## References

- Bahcall DO, Kowler E (1999) Illusory shifts in visual direction accompany adaptation of saccadic eye movements. *Nature* 400:864–866.
- Becker W, Jürgens R (1990) Human oblique saccades: quantitative analysis of the relation between horizontal and vertical components. *Vision Res* 30:893–920.
- Chen-Harris H, Joiner WM, Ethier V, Zee DS, Shadmehr R (2008) Adaptive control of saccades via internal feedback. *J Neurosci* 28:2804–2813.
- Goossens H, van Opstal AJ (2006) Dynamic ensemble coding of saccades in the monkey superior colliculus. *J Neurophysiol* 95:2326–2341.
- Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. *Nature* 394:780–784.
- Harris CM, Wolpert DM (2006) The main sequence of saccades optimizes speed-accuracy trade-off. *Biol Cybern* 95:21–29.
- Harwood MR, Mezey LE, Harris CM (1999) The spectral main sequence of human saccades. *J Neurosci* 19:9098–9106.
- Jürgens R, Becker W, Kornhuber HH (1981) Natural and drug-induced variations of velocity and duration of human saccadic eye movements: evidence for a control of the neural pulse generator by local feedback. *Biol Cybern* 39:87–96.
- McSorley E, Haggard P, Walker R (2006) Time course of oculomotor inhibition revealed by saccade trajectory modulation. *J Neurophysiol* 96:1420–1424.
- Port NJ, Wurtz RH (2003) Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *J Neurophysiol* 90:1887–1903.