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Oculomotor Hide and Seek: Pursuing an Accelerating Target Behind an Occluder. Focus on "Target Acceleration Can Be Extracted and Represented Within the Predictive Drive to Ocular Pursuit"

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Smooth pursuit eye movements are used to maintain the image of a moving object on the fovea. In the laboratory, most smooth pursuit studies are conducted with a target that travels at a constant velocity in clear view. In this situation, visual feedback created by the target's motion on the retina allows the pursuit system to keep the fovea directed toward it. However, most objects moving in a natural scene accelerate or decelerate, and often their path is occluded by other objects. The problem of pursuing a real object becomes even more vexing for the pursuit system because of the well-known difficulty of humans to perceive acceleration, and evidence that smooth pursuit suffers from the same limitation. In the paper by Bennett and colleagues (2007), in this issue of *Journal of Neurophysiology* (p. 1405–1414) the authors investigate pursuit of accelerating targets that disappear behind a virtual occluder. Here, they present novel data showing that the pursuit system can estimate where an accelerating target will appear and how fast it will be moving after the occlusion.

In the paper, the authors entertain three hypotheses. The first is a "final velocity" hypothesis, in which observers use the velocity of the target immediately before it disappears to estimate its velocity when it reappears. This hypothesis is based on the prediction of pursuit models that an efference copy signal generated by recent pursuit of a target can maintain eye velocity for a short duration. The second is an "average velocity" hypothesis in which average target velocity over the preocclusion viewing period is used to estimate the speed of the target on reappearance. The third "acceleration" hypothesis states that the acceleration of the target is computed by the pursuit system and that this computation guides the eyes after the occlusion.

To test between these hypotheses, observers were presented with a target that moved at different initial speeds, but maintained a constant acceleration throughout each trial. The target was visible for either a brief interval (200 ms), or a longer one (500 or 800 ms), before disappearing from view behind a virtual occluder for 500 ms. The task was designed so that the different target velocities were independent of target acceleration at the time of target disappearance, and the mean target velocity during any interval of the initial visible ramp (except the final 50 ms) had an inverse relationship with target acceleration. Design of the experiment is clever, in that it disambiguates target acceleration, average target velocity, and final target velocity before target disappearance, allowing a clean test of the three hypotheses. When preocclusion target viewing was limited to 200 ms, subjects were unsuccessful at matching the appropriate acceleration after the occlusion. However, with the longer 500- or 800-ms viewing times, their pursuit eye movements discriminated between the different accelerations when the target reappeared. Not only did smooth velocity during pursuit contribute to estimating target acceleration, saccades were also used to correct for virtual position error that developed. Although the results support the acceleration hypothesis, even the combined response did not completely eliminate retinal image slip and position error at the time of target reappearance.

That the oculomotor system appeared to derive a coarse estimate of target acceleration in this study is important because the notion that acceleration can guide smooth pursuit is controversial. Reflecting this, one prominent model of pursuit incorporates acceleration analyzers (Krauzlis and Lisberger 1989), whereas another does not (Robinson et al. 1986). The motion-perception system is poor at determining the acceleration of moving objects, in that it can discriminate only between accelerations that differ by about 100% (Watamaniuk 2003). Because there is evidence that pursuit receives input from the same motion-processing substrate as the perceptual system (Beutter and Stone 1998; Madelain and Krauzlis 2003; Stone and Krauzlis 2003; Watamaniuk and Heinen 1999), the pursuit system potentially suffers a similar liability. In support of this, neurons in the middle temporal cortex (MT), a region specifically involved in motion processing (Dubner and Zeki 1971; Rodman and Albright 1987; Tootell et al. 1995) and motion perception (Britten et al. 1996; Liu and Newsome 2005; Newsome et al. 1989), do not show acceleration sensitivity (Lisberger and Movshon 1999; Price et al. 2005). However, it is possible to construct an acceleration signal from the population (Lisberger and Movshon 1999; Price et al. 2005). Previous work on acceleration sensitivity of the pursuit system demonstrated that it can detect whether an object is accelerating (Krauzlis and Lisberger 1994). However, the ability of this system to discriminate between different nonoccluded accelerations is poor (Watamaniuk and Heinen 2003). Results of the current study are consistent with this and show that, despite an occlusion, a rough estimate of acceleration can be accessed by the pursuit system.

Another important contribution of this study is that it describes the response of the saccadic system to accelerating target motion. Saccadic intrusions during smooth pursuit are common and are not simply driven by position error, but rather by a host of factors such as target and pursuit velocity (de Brouwer et al. 2002a,b; Keller and Johnsen 1990). Therefore coordination between the pursuit and saccadic systems during pursuit of constant velocity motion appears to be intricately choreographed. In support of this, there is evidence that these

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systems are privy to the same motion signals and are subserved by similar neuronal substrates during pursuit of constant velocity motion (for reviews see Krauzlis 2004; Krauzlis and Stone 1999). Therefore it is a natural extension of previous work to investigate the sensitivity of both systems to accelerating targets. Whereas some work has shown that pursuit and saccades can estimate target velocity after occlusion (Orban de Xivry et al. 2006), this paper demonstrates for the first time that the smooth and saccadic systems coordinate to estimate the acceleration of targets that are occluded.

Given that the pursuit system does not accurately extract acceleration from the motion of a target, how might it derive the coarse acceleration estimate it does in the current study? The authors suggest a reasonable explanation—that the system samples velocity in a sequential fashion by comparing a previous velocity sample with the current one. This idea has been shown to explain how anticipatory pursuit eye movements are generated (Barnes and Asselman 1991; Barnes and Schmid 2002; Collins and Barnes 2005). Such a mechanism is also capable of approximating the acceleration and deceleration of sinusoidal target motion (Barnes 1994; Barnes et al. 2000). Comparing successive velocity samples could be the method we use when orienting the eyes or other effectors to objects that accelerate in natural scenes.

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