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SHORT AND SWEET

Eyes pursue moving objects, not retinal motion signals

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Abstract. For smooth-pursuit eye movements, a moving target is necessary, but we show that it is not sufficient. Observers pursued targets that appeared to move in one direction even though they really moved in another. Changes in perceived direction did not disrupt pursuit eye movements, but motion-based failures in object parsing did.

Pursuit eye movements are the smooth rolling movements of the eyeball that lock a moving target onto the high-acuity fovea (Kowler 1990). Is this a simple tracking servo system, driven by error signal from retinal slip? Or is it a sophisticated, cognitive system, receiving the same visual inputs as does motion perception? (Beutter and Stone 2000; Krauzlis 2004; Barnes 2008). We measured attempts to pursue objects that moved in one direction but, under the influence of three separate motion illusions (flying bugs, chopsticks, and rings: Anstis 1990, 2003; Anstis and Casco 2006), appeared to move in a different direction. We argued that a retinal-slip servo would track the physical motion, whereas a perception-based top – down system would track the perceived motion.

Six movies of these illusions are available in the supplementary materials (see http://dx.doi.org/10.1068/p6429). In the flying-bugs illusion (Anstis and Casco 2006), a bug or small spot circled clockwise on a large background that was circling counterclockwise without rotating. Induced movement (Duncker 1929/1938; Reinhardt-Rutland 1988) from the background made the bug's circular path look like an illusory elongated ellipse, tilted at 45°. Three observers either attempted to pursue the moving bug with their eyes, or else adjusted the Lissajous path of a separate matching spot, to match the illusory trajectory. Figure 1 shows that they perceived the bug's path as elliptical (dotted ellipse shows the best fit to their mean settings). Their pursuit eye movements accurately tracked the bug's circular orbit (the circle in figure 1 shows the best fit to their eye movements that are shown in figures 2a and 2b), but when questioned, they claimed that their eyes were moving around an elliptical path rather than the actual circular path. *Conclusion*: They were not aware of what their own eyes were doing. Evidently awareness of eye movements, even if based on efference copy (Holst and Mittelstaedt 1950; Perrone and Krauzlis 2008), is substantially modulated by retinal feedback. The accuracy of the smooth pursuit despite strong reports of perceptual illusion has been reported before, even, recently, in monkeys (Zivotofsky et al 2005). Moreover, an earlier paper showed that the eye tracking was unaffected by the illusion but head movement was (Zivotofsky et al 1995).

In the chopstick illusion (Anstis 1990, 2003, 2007), a horizontal and a vertical line overlapped to form a cross (figure 2c). The lines moved along counterphase clockwise paths at 0.88 revolutions s^{-1} without rotating. The centre of the cross, where the lines intersect, actually moves along a *counterclockwise* Lissajous circle, but observers nearly always perceive it as moving *clockwise*, with the lines sliding over each other.

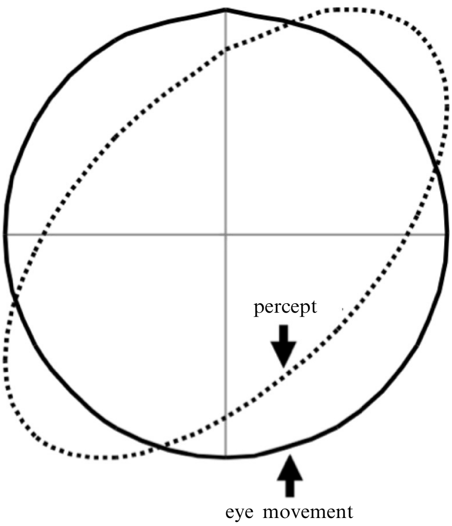

Figure 1. Perceived and pursuit paths in the flying-bug illusion (movie versions are in the supplementary materials). The bug, and the pursuit movements (also shown in figures 2a and 2b), actually moved in a circle (Lissajous phase shift = 90°). But observers believed that the bug and their eyes followed the illusory tilted ellipse (phase shift = 55°).

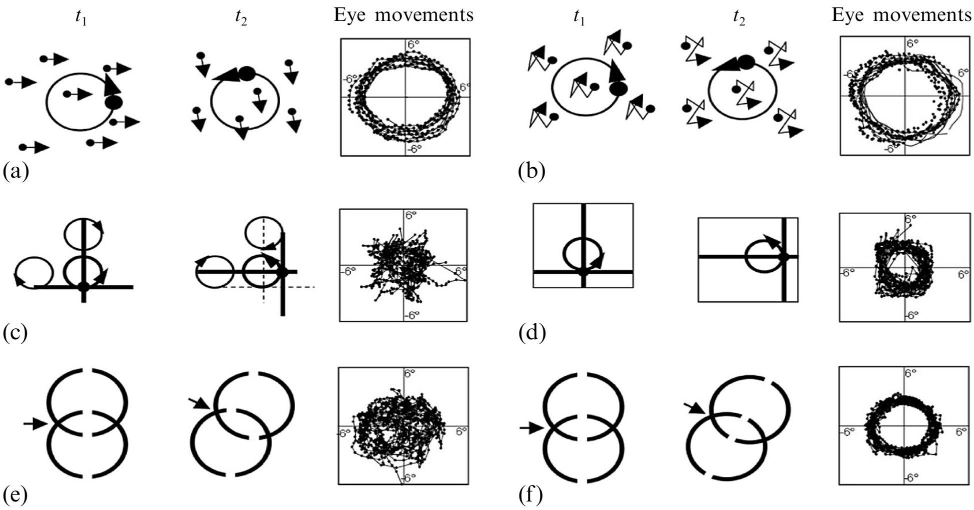

Figure 2. Illusory motion stimuli and typical tracking eye movements. Movie versions are in the supplementary materials. (a) and (b) A bug flying in counterclockwise circles was accurately tracked with circular eye movements. When the background jittered randomly (b), the observers correctly saw the bug and their eyes as moving in circles. When the background circled clockwise (a), they incorrectly believed that the bug and their eyes were following a right-oblique ellipse. *Conclusion*: They did not know how their eyes were moving. (c) Circling chopsticks appeared to slide and apparently circle clockwise. Eye tracking was very poor. (d) The same chopsticks with a moving frame were parsed as a rigid cross circling counterclockwise. Eye tracking was good. (e) Rotating rings with vertically aligned gaps or spots appeared to slide. Observers could not track sliding intersection (arrowed). (f) Rings with painted-on spots were parsed as a solid figure of eight. Now observers could track rigid intersection (arrowed).

We believe that the clockwise motion of the line tips propagates along the lines and is blindly assigned to the central intersection (see McDermott and Adelson 2004). Five observers made large errors when they attempted to pursue this sliding intersection (figure 2c). This illusion disappears instantly, and accurate pursuit movements are restored, if a floating square frame is added that just touches the ends of the lines (figure 2d). Now the lines are correctly parsed as a rigid cross rotating counterclockwise, with no sliding, because, even though in figure 2d the circling tips are always visible, they are interpreted as being occluded by the square frame (Shimojo et al 1989), so are not taken as a reliable guide to the movements of the lines. We argue that the changed status of the line terminators makes the intersection easier to track. With the counterrotating terminators out of the picture, both remaining elements, the intersection and the frame, rotate in the same direction. However, the frame moves 180° out of phase with the intersection, being at 6 o'clock when the intersection is at 12 o'clock, so any attempt to track the square frame itself would disrupt rather than improve tracking of the intersection.

Root-mean-square tracking errors were calculated as the SD of the eye movement radii, divided by the mean radius. Removing the frame from the chopsticks increased these errors by $\sim 50\%$, from 0.30 to 0.433 ($F_{1,16} = 10.978$, $p < 0.01$).

We now modified the chopstick illusion into a sliding-rings version. We removed the line terminators (tips) by bending the lines around into rings that rotated at 0.45 revolutions s^{-1}. Two gaps or spots on each ring acted like terminators. When these spots rotated with the rings (figure 2f), three observers reported a single rigid rotating figure of eight, and they could successfully pursue the X-shaped junction (arrowed in figures 2e and 2f) where the two rings intersected. But when the two spots on each ring always remained vertically aligned, somewhat like a floating compass needle (figure 2e), the percept was radically reorganized into two separate rings that slid over each other. Ability to pursue the sliding X-shaped intersection with the eyes fell off markedly and the rms tracking errors doubled from 0.147 to 0.291 ($t = -6.156$, $p = 0.025$).

The chopstick/ring illusion has a different mechanism from the bugs illusion. Although both illusions comprise overlapping interacting circular orbits, the bugs illusion involves motion contrast, in which a moving spot seems to go in the opposite direction to other objects. The chopstick/ring illusion involves motion assimilation, in which a moving intersection seems to go in the same direction as other parts of the same assembly (Spering and Gegenfurtner 2007). Crucially, the chopstick and ring illusions disrupted pursuit eye movements where the bugs illusion did not. Thus, in the bugs illusion, observers accurately tracked the circular orbits of the bugs, but they misperceived both the bug paths and their own eye movements as being elliptical. In the chopstick illusion, framed intersections (figure 2d) were parsed as rigid objects and could be successfully tracked, but without the frame (figure 2c) the very same intersections were parsed not as objects but as incoherent sliding junctions, and they could no longer be well tracked. Likewise, rigidly intersecting rings could be tracked but sliding ring junctions could not (figures 2e and 2f). The local retinal signals from intersecting lines or rings were the same whether they were rigid or sliding, so clearly these pursuit movements were not simply driven by retinal slip.

So what disrupts the pursuit eye movements? Not just illusory changes in direction, since the bugs are perceived to deviate from their true direction but can be tracked, whereas the sliding ring intersections appear to follow their true, circular, path and yet cannot be tracked. It is the failure of object parsing that upsets pursuit. Bugs are seen as objects and can be pursued, and so can perceptually rigid intersections, whereas the sliding intersections of rings and lines are not parsed as objects and cannot be pursued. We conclude that pursuit eye movements are not a simple tracking servo, but receive sophisticated top–down control from object parsing (Beutter and Stone 2000; Krauzlis 2004; Barnes 2008). A visual control system that can dismiss intersecting tree twigs as noise, but can correctly parse and track even the stealthiest moving predator, is likely to survive.

Guide to the movies in supplementary materials

Six movies are attached, each about 6 Mb in size:

1. BugStim.mpg shows a circling yellow bug, first against a rotating background (figure 2b: the bug's path appears to be an ellipse), then against a randomly jittering background (figure 2a: the bug's path is correctly seen as circular).

2. BugEM.mpg shows the same stimuli as #1, with typical eye movements superimposed as a red trail.
3. ChopsticksStim.mpg shows the chopsticks circling counterclockwise, first on their own (figure 2c: the central intersection appears to move clockwise), then with a floating square frame (figure 2d: intersection correctly seen as circling counterclockwise).
4. ChopstickEM.mpg shows the same stimuli as #3, with typical eye movements superimposed as a red trail. For convenience a blue disk (never seen by the observers) indicates the target intersection they were trying to track.
5. RingsStim.mpg shows the sliding rings, first floating (figure 2e: hard to track) then painted on the rings (figure 2f: easy to track).
6. RingsEM.mpg shows the same stimuli as #5, with typical eye movements superimposed as a red trail. Blue disk indicates the target intersection they were trying to track.

See also the GuideToVideoMaterials.ppt in the supplementary materials.

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