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PURSUING THE PERCEPTUAL RATHER THAN THE RETINAL STIMULUS

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Abstract—In the first experiment, subjects were able to successfully track a perceptually completed contour that was extrapolated from peripheral retinal information. In the second experiment, subjects successfully pursued an object that moved horizontally behind a narrow slit in such a way that the only visible stimuli were the edges of the object moving vertically in the slit. In the third experiment, subjects successfully tracked the invisible center of a rolling wheel when all that could be seen were points of light travelling in a cycloidal path on the rim of the wheel. It is argued that the stimulus for pursuit eye movements is the appreciation of an object in motion with respect to the observer, regardless of the retinal stimulation, and in some cases regardless of the sense modality through which the motion is detected.

What is the stimulus for pursuit eye movements? The traditional statement is that a moving retinal image at or very near to the fovea is required before pursuit can be released. And yet, a number of studies show that retinal motion may not be necessary for pursuit (e.g. Gertz, 1916; Heywood, 1973; Richards and Steinbach, 1972; Steinbach and Pearce, 1972; Steinbach, 1969). I would like to suggest that the fundamental requirement for pursuit is the *appreciation of an object in motion with respect to the observer* irrespective of retinal stimulation, and in some cases irrespective of the sense modality through which motion is assessed. The experiments described below show pursuit being elicited in a variety of situations where the retinal stimulation provides what is usually thought to be inadequate and inappropriate information for the direction and extent of the eye movements actually made.

EXPERIMENT 1

There have been a number of demonstrations that, when presented with incomplete figures, the visual system may perceive "contours" in regions where there is no retinal stimulus (e.g. Coren, 1972; Gregory, 1972; Tynan and Sekuler, 1975). Can the visual system use such a "cognitive" contour as a target to be pursued? The first experiment shows that this can be an effective pursuit stimulus.

Method

The stimulus field consisted of a large opaque white occluder (44 cm from the subject's eye) which extended 60° (in visual angle) horizontally and 30° vertically. Just behind the occluder was a white diamond (17 cm on a side) mounted so that it could be moved through a visual angle of 38°. The diamond was suspended on a framework that allowed its horizontal displacement to be monitored using a potentiometer. The corner of the diamond was 13° away from the nearest edge of the occluder and thus the only motion stimulus present for the observer if his eye were directed at the apparent location of the occluded corner would be at least 13° away from the fovea (see the top of Fig. 1).

The horizontal movements of one eye were measured by a photoelectric method (Biometrics: Model SG/H). Viewing was binocular. Because this system does not accurately measure vertical eye movements, and because the vertical positioning of the eye is so crucial in this experiment, an after-image method of assessing vertical eye position was used. The opaque occluder had a round (1.2° dia) aperture placed to the right of the limit of movement of the hidden corner of the diamond, and at the same horizontal level. An intense electronic photo flash was placed just behind this aperture. The experimenter triggered the flash when he noticed a horizontal pursuit eye movement signal on a chart recorder. The flash created a very strong after-image, the position of which corresponded to the position the eye was in when the flash occurred. The location of the after-image relative to the fovea was immediately measured by having the subject

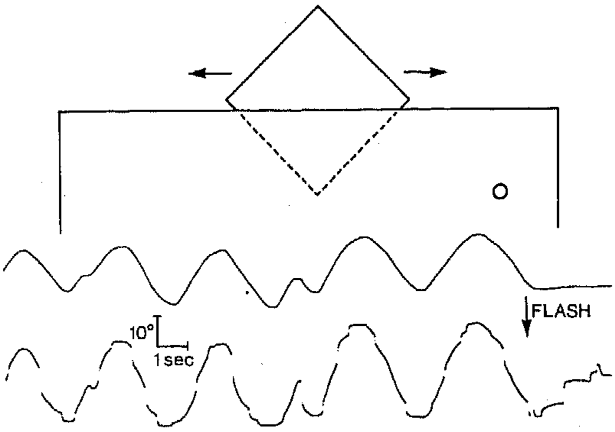

Fig. 1. Top portion shows stimulus configuration for Experiment 1. Subjects were instructed to track the occluded corner of the diamond which was moved back and forth by the experimenter in an irregular manner. A flash triggered behind the circular aperture produced an after-image used to assess the subject's vertical eye position. The bottom half shows the target movement trace (top) and eye movement trace (bottom) as the subject tracked the apparent location of the corner. The after-image formed at the flash onset, during a clear episode of horizontal pursuit, confirmed that the visual axis was at the same horizontal level as the apparent location of the corner.

mark the location of the after-image on a sheet of paper while fixating a cross inscribed on the paper. This measure was used to check the accuracy of the horizontal eye movement record and also to detect any vertical deviation of the eye from the path of movement of the corner of the diamond. The flash onset was recorded on the chart recorder along with eye and target movements. The subject's head was steadied using a mouth bite with dental impression material.

Subjects and procedures. Subjects were paid graduates and undergraduates at York University. All subjects could perform the task without spectacle correction. Twelve subjects participated.

Each subject had his eye position calibrated using the diamond placed in front of the occluder. This also familiarized the subject with the stimulus materials and in particular with the stimulus configuration that would exist behind the occluder. After calibration, the diamond was placed behind the occluder so that its bottom half was covered, and the subject was instructed that the experimenter would be moving it back and forth irregularly and that his task was to track the corner of the diamond as if he could see it, just as he had been doing in the calibration procedure. The subject was cautioned not to let his gaze drift up to where the edge of the card sheared the top of the occluder. After 30–60 sec of tracking, the experimenter triggered the flash during a pursuit movement (when the center of gaze was near the flash aperture so that the after-image would not be too far in the periphery and thus be difficult to see and locate). A piece of paper was then placed in front of the subject, and a strobe light turned on (about 2 Hz) to make the after-image easier to see. The subject fixated on the cross on the paper and marked the after-image location with a felt-tipped pen. After 4 or 5 min the after-image was completely faded and a new trial began. Three to five trials comprised a session.

Results

All subjects were able to pursue the apparent corner without difficulty. In almost all of the trials, there was no or little vertical misalignment of the eye from the level of the occluded corner. Figure 1 shows 20 sec of pursuit of one subject whose visual axis was directed at the level of the occluded point when the flash occurred. The tracking has some saccades, but these are likely to be present when any irregularly moving target is pursued (Steinbach and Held, 1968). The pursuit in all instances was easy to elicit. The reader is invited to try the experiment himself by moving an index card behind an opaque card and having someone else note the type of eye movements made while the visual axis is directed at the occluded corner.

Discussion

Objection can be raised to the demonstration of pursuit in this experiment on the grounds that there is a peripheral stimulus moving in the same direction and manner as the occluded point the subjects are asked to track. Is a peripheral target sufficient to drive pursuit? Optokinetic nystagmus (OKN) occurs in response to large moving patterns in the periphery. The response revealed in this experiment may represent the slow phase of such a peripherally-driven OKN. However, Hood (1967) showed that peripherally-driven OKN has a higher velocity than foveally-driven OKN, and in the experiments reported above, the pursuit velocities were appropriate to the movements of the occluded corner, as though the tracking was foveally driven. Cheng and Outerbridge (1974) also showed that peripheral OKN has characteristics which differ from those found here.

It is still possible that pursuit may be driven by stimuli well off the fovea. Indeed, Spillman (1964) noted that some subjects in his experiment could do it, though only with great difficulty and with fatigue quickly occurring. Steinman, Skavenski and Sansbury (1969) noted that some subjects were able to track at velocities less than that of the target, thus, in effect using peripheral stimuli. In Spillman's experiment and in Steinman's experiment as well as in Experiment I above, tracking movements were always in the same direction as the movement of the stimuli—in all cases horizontal. The next experiment shows that horizontal pursuit can occur when the only stimulus present on the retina is moving *vertically.*

EXPERIMENT 2

If a figure is moved horizontally behind a narrow vertical slit, the figure will eventually appear to be compressed laterally. There has been debate about whether or not the illusion is due to the effects of pursuit eye movements causing the retinal image of the moving object to be "painted" across the retina, or due to some higher order, cognitive storage effect. Helmholtz subscribed to the first view (see Anstis and Atkinson, 1967), and Parks (1965) holds the latter view. The experiments by Rock and Halper (1969) and the demonstration of Parks (1970) indicate that eye movements are not the cause of the illusion and that higher cognitive functions are critical. Note that in this type of experiment the subject *perceives an object moving horizontally behind a narrow vertical slit.* The important question in the present context is whether the subject is able to smoothly pursue such a horizontally moving object when the only stimulus on the retina is moving vertically. A sufficiently narrow slit should allow no useful horizontal component of motion to be seen.

Method

Using a cathode ray oscilloscope (CRO) an ellipse was displayed tilted 45° to the right, with a major axis of 3.9° and a minor axis of 1.8°. It could be driven to and fro horizontally over a 3° excursion at a rate of 1 Hz. Covering the CRO and ellipse was an opaque sheet with a 6′ wide vertical slit cut into it at the midline. The viewing distance was 114 cm.

Eye movement monitoring was accomplished using a tightly fitting scleral contact lens that for one observer (the author) was molded to the shape of his eye, and for the other observer (BJR) was a modified ERG lens (Medical Workshop Lens LOVAC Model) that could be very firmly applied with negative pressure. The lenses had small plane mirrors mounted in them so that an optical lever (a helium neon laser beam) could be reflected onto a photodiode that was sensitive to horizontal and vertical positions of the laser beam (United Detector Technology Model SC-50). The system as used in this experiment had a range of about 4° horizontally and vertically and a resolution of 5′. Subjects viewed the CRO display monocularly, and the spectacle correction for MJS was incorporated into his lens. The head was steadied with a sturdy dental impression bite bar.

The subject pressed a button when he perceived the stimulus configuration to be an ellipse moving behind a

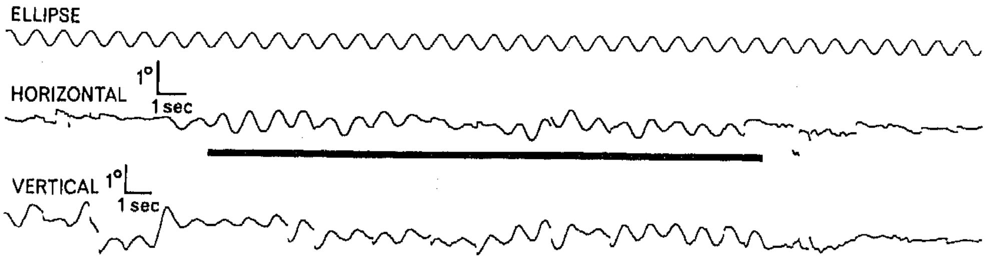

Fig. 2. Horizontal and vertical component of eye movements measured by an optical-lever contact lens technique and made while the subject tracked an ellipse (tilted at 45°) moving horizontally behind a narrow vertical slit. Driving function for the ellipse is on the top trace. The heavy black line shows when the subject perceived the stimulus as an ellipse moving behind a slit, rather than two spots of light moving vertically in counterphase. The occurrence of horizontal pursuit is correlated with the percept of an "object" seen moving behind the narrow slit.

slit. The subject's response, the movement of the ellipse, and the vertical and horizontal eye movements were each recorded on separate channels of a chart recorder.

Results

Figure 2 shows a representative record for MJS. The most obvious finding is the correlation of horizontal pursuit with the subject's report of the percept of an ellipse moving behind the slit. Prior to the subject's report of an ellipse, and just after it ended, the absence of horizontal pursuit is readily seen. When not seeing the ellipse, the subject reported seeing two spots moving up and down vertically, "bumping" in the middle, and his eyes showed vertical pursuit movements. These vertical pursuit movements were also evident, along with the horizontal pursuit, when the subject reported seeing a moving ellipse. The fact that the vertical and horizontal pursuit movements occur together may be related to the fact that the subject interpreted the ellipse tilted at a 45° angle as moving obliquely. The horizontal component, however, is critical in this demonstration because there was essentially no horizontal motion in the retinal stimulus.

The other subject (BJR) provided similar records. For both subjects there was a latent period when the ellipse was not seen which was accompanied by vertical eye movements. This was followed by the growth of the percept of an object moving behind the slit which then elicited the horizontal component of the pursuit movement.

The experiment was also done using a circle moving behind the slit, rather than the tilted ellipse. The same pattern of horizontal pursuit movements accompanied the occurrence of the subjects' perception of an object moving behind the slit. The subject saw an ellipse whose major axis was vertical in this instance, and no oblique tracking occurred.

EXPERIMENT 3

Wallach (1959) has pointed out that we are generally unaware of the path taken by different points on moving objects. His best example, first described by Duncker (1929), concerns the rolling motion of a wheel: the path of a point on the rim of a rolling wheel is a series of cycloids (see top of Fig. 3). If a subject can see only a single light attached to the rim of a rolling wheel, he will see the cycloids but will be totally unaware of any rolling, wheel-like motion. When a light on the hub can be seen in addition to the rim light the percept is immediately one of rolling motion and the cycloidal motion of the rim light is no longer perceived. If a second rim light is used instead of the hub light, the percept is still that of a rolling wheel, and the hub or center of rotation can be imagined. This imagined center of rotation was the pursuit stimulus of the third experiment.

Method

Two small (1 mm dia) red Light-Emitting Diodes (LEDs) were mounted at opposite sides of an 8.6 cm wheel. The wheel rode in a track 34 cm long in the frontal plane, 72 cm

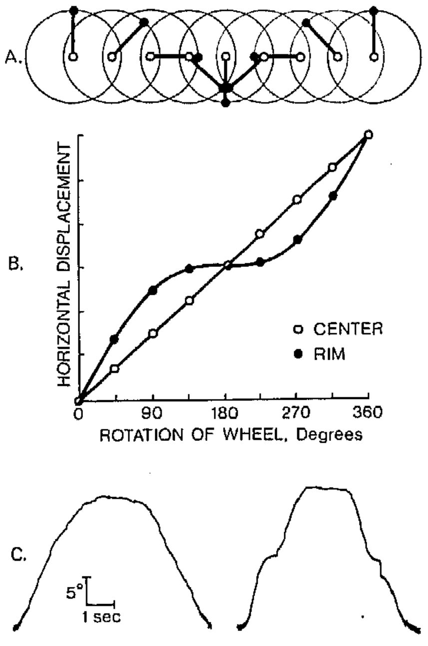

Fig 3. A: Locus of points on the rim and hub of a wheel that rolls through one revolution. B: Horizontal displacement of points on the rim and hub of a wheel that rolls through 360°. C: Typical horizontal eye movement records of a subject's attempts to track the centre of rotation through movement of wheel first to the left and then to the right. In the left trace two rim lights diametrically opposed were visible; in the right trace only one rim light was on. In both instances the lights traversed cycloidal paths (as depicted in the rim path in B), but when two cycloids 180° out of phase were present, the subject perceived a rotating wheel and was able to track the imagined centre. With only one rim light on, no percept of a rolling wheel was formed and the subject resorted to tracking that single light through the cycloid path.

away from the subject's eye. With one LED on in an otherwise dark room, just over one cycloid was displayed to the subject as the wheel rolled from one end of its track to the other. With both LEDs on, two cycloids, 180° out of phase and separated by the diameter of the wheel were displayed to the subject.

The experimenter moved the wheel back and forth over the track and attempted to maintain a constant linear velocity of about 10 deg/sec over most of the movement.

Seven subjects, staff at the Smith–Kettlewell Institute of Visual Sciences, were observers. They were instructed to track the hub of the wheel rolling in the dark when either one or both rim LEDs were on (they observed the apparatus in the light and were thus aware of how the moving stimuli were generated).

Eye movements were measured photoelectrically (Biometrics) and the head held steady with a combination chin and forehead rest.

Results and discussion

With only one rim light on, subjects did not perceive a rolling motion, and were unable to imagine the hub. Their eyes did not therefore track the motion of the hub. However, with the two rim lights on, all subjects had the percept of a rolling wheel and all could, with ease, track its imagined center. Representative eye-movement records for one subject are shown in Fig. 3, but before they can be understood we must first consider an analysis of the horizontal component of displacement as the wheel rolls through one revolution. Figure 3B shows a graph of horizontal displacement for a point on the rim and a point on the hub of a wheel rolled through 360°. Figure 3A shows points on the hub and rim as it would actually be seen rolling through one revolution. If the wheel rolls at a constant velocity, the hub moves horizontally at a constant velocity also, as indicated by the diagonal line in Fig. 3B. If, however, the rim point is traced in its horizontal excursion while the wheel rolls with constant horizontal velocity, we see that, during one rotation of the wheel, it initially moves with greater velocity than the hub, is then slowed down until it lags *behind* the hub, and finally again overtakes the hub, at the end of the rotation.

The eye-movement patterns shown in Fig. 3C on the left occurred when two rim lights were on and the subject tracked the imagined center of rotation. The record on the right resulted from the situation in which just one rim light was on and the subject attempted to track the center of rotation. As noted above, with only one light on the rim, wheel-like motion is not experienced, and all subjects resorted to pursuing the single rim dot moving in a cycloid, with the resulting distortions of horizontal velocity predicted in Fig. 3B.

With two rim lights, the compelling perceptual experience is of a rolling wheel. The motions of parts of a moving object relative to a stationary point are very difficult to see. In such a case, one responds to the spatial invariance between the moving parts, and perceives a single coherent motion of a rigid body (Johansson, 1975).

GENERAL DISCUSSION

The experiments presented above indicate that the occurrence of pursuit eye movements depends on the observer's appreciation of a moving object, rather than on the scraps of sensory information which lead to the percept. In Experiment 1 the cognitive contour, extrapolated from peripheral retinal information, was sufficient to elicit pursuit. In Experiment 2, pursuit eye movements which were "inappropriate" in terms of the retinal stimuli occurred when a percept was formed of an object moving horizontally behind a narrow slit. In Experiment 3 "inappropriate" eye movements were also made to track the imagined centre of a rotating wheel when the retinal stimuli were points of light moving in a cycloid.

Non-visual information can also provide one with an adequate stimulus for pursuit. It has been known for some time that a person can pursue his own hand in the dark (Gertz, 1916; Gregory, 1957; von Noorden and Mackensen, 1961; Steinbach, 1969). Figure 4 shows 12'sec of one observer's attempts to smoothly track his own hand in darkness (eye movements were recorded with a photoelectric method; hand movements with a potientiometer coupled to the moving arm). The record is interrupted by saccades yet the smooth nature of segments in between saccades is obvious. In fact, if the smooth sections are joined up, as was done in the bottom trace of Fig. 4, the smooth signal that was sent to the oculomotor system is revealed, which can be seen to correlate with the hand movement signal. The saccades appear superimposed on this smooth signal and this coincides with previous descriptions of the independence of the smooth and saccadic systems (Robinson, 1965; Jurgens and Becker, 1975).

What is generally not appreciated is the range of individual differences encountered in the ability to track the unseen hand. As the author first noted in 1969, the individual differences were much reduced when subjects were provided with brief glimpses of the hand by stroboscopically illuminating it.

Figure 5 shows the facilitation of hand tracking by intermittent visual information about hand position. In the top half, the subject who was attempting to track her own hand in the dark produced occasional brief episodes of pursuit, but mostly large saccades. In the bottom half of the figure, the records were taken when the subject's hand was strobe-illuminated at 1 sec intervals. The dramatic increase in pursuit is obvious and represents the typical result for those subjects having difficult producing pursuit when tracking their own hand in complete darkness. Why should pursuit be readily elicited when there is no *retinal* motion cue? The obvious additional source of information being used by the oculomotor system in this instance derives from proprioception.

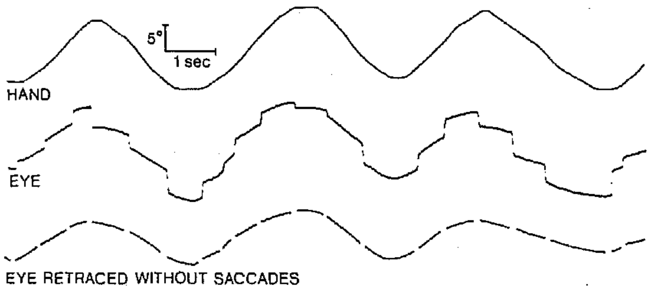

Fig. 4. Subject tracking own hand in complete darkness. The bottom trace shows the smooth sections of the middle trace redrawn and joined together without saccades.

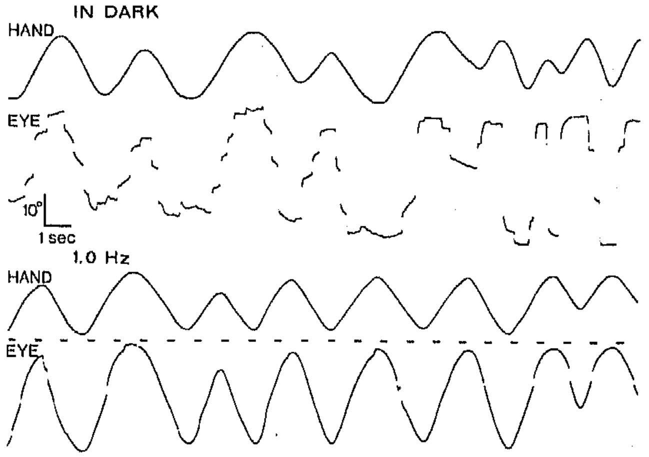

Fig. 5. Top pair of traces shows subject's attempt to track her own hand in complete darkness. There are some short episodes of pursuit, but tracking is mostly saccadic. Bottom pair of traces shows the marked improvement in pursuit that occurs when the hand is strobe-illuminated (μsec pulses) at 1 Hz.

Gauthier and Hofferer (1976) have recently shown how effectively this cue can elicit pursuit when a subject is attempting to track his hand in the dark. Steinbach (1969) demonstrated the contribution of efference (outflow), although these results did not conflict with the notion that the largest contribution to the motion signal that the oculomotor system must use to produce pursuit comes from inflow or proprioceptive sources.

The fact that a person can pursue his strobe-lit hand meshes with an observation made by MacKay (1961). He first described a powerful illusion of movement that occurred when self-luminous objects imbedded in a background, were moved with the background and strobe-illuminated. At the proper strobe rate (5–10 Hz), the luminous targets appeared to slide around and even wander off the background surface. (This is due to the fact that strobe illumination of the background provides discontinuous information of the background while there is continuous information about the position and movements of the luminous spot within it.) The observation of interest here is that the illusion weakens or disappears if the observer moves the light and background himself. MacKay suggested that this reduction of the illusion occurs because the observer now has continuous information about the movement of the background from proprioceptive sources and can "fill-in" between the strobe flashes. This suggested explanation is strongly supported by the evidence cited above.

Westheimer (1954) and von Noorden and Mackensen (1961) have shown that stroboscopically illuminated targets can be pursued with flash intervals between 50 and 200 msec, i.e. at rates that produce the perception of phi movement. However, in the studies reported above, in which it was shown that pursuit movements do not occur in response to stroboscopically illuminated targets in the absence of proprioceptive information about target motion, phi movement was not a factor because the strobe rate was so low that apparent visual motion was not perceived (Steinbach, 1969).

Can the motion of objects be assessed through other modalities? Gibson (1968) has suggested that motion can be regarded as an "amodal" concept, i.e. some higher order construct that is not dependent on the type of sensory information received. Gertz (1916) describes subjects smoothly tracking sound sources and also tactile stimuli with their eyes. In attempting to replicate these experiments, I found considerable individual differences in the ability to smoothly track these non-visible sources. The ability to track moving sounds or motion sensed proprioceptively may represent some underlying capacity to "visualize". Experiments have shown that people vary in their capacity to visualize motion (e.g. Brown, 1968). People who can track their own hand in darkness are generally able to also track a moving sound source. This ability seems to be trainable because the quality of pursuit eye movements have been found to improve with practice.

The role that *intent* plays in pursuit has not been adequately investigated. In the presence of moving objects (apart from the unnatural, large-field OKN stimulus) pursuit is not obligatory; it is "voluntary" in the sense that it must be initiated by the observer who wishes to track an object. Ter Braak (1972) has clearly shown how important intent can be when the observer is provided with ambiguous motion information.

Dimitrov, Yakimov, Mateef, Mitrani, Radil-Weiss and Bozkov (1976) have shown that saccades can be made to corners of a stationary plane that does not exist monocularly (they used random dot stereograms, "Julesz figures"). An obvious extension of this experiment for the present argument would be to move the Julesz plane and to see if it could be tracked. It is known that moving Julesz planes can produce motion after-effects (Papert, 1964) so almost certainly there will be pursuit of this moving surface. In terms of the monocular stimulation reaching each eye in such a dynamic random dot pattern, there will be no stimulus to track, but binocularly there will be a clearly moving object. If people are able to track such a moving object, and preliminary results indicate that this is so (Anstis and Steinbach, in preparation), it is consistent with the arguments made here that retinal events are of marginal importance in determining pursuit onset.

The results from the three experiments suggest that servo-mechanical models of the pursuit system that operate on retinal shear velocities or foveal lag are far too simple. The pursuit system is turned on by a centrally-derived motion percept which, as these experiments demonstrate, can be far removed from a simple analysis of retinal events.

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