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LETTER TO THE EDITORS

RELEASE OF PURSUIT EYE MOVEMENTS USING AFTER-IMAGES[1]

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IT IS frequently asserted that a moving visual target is necessary in order for the eyes to make slow, conjugate pursuit movements (e.g. ROBINSON, 1968). There are, however, violations to this fiat (see, e.g. RICHARDS and STEINBACH, 1972; YOUNG, 1971). Some subjects can smoothly track their own moving hand in complete darkness (STEINBACH, 1969; VON NOORDEN and MACKENSEN, 1962), indicating that an internal proprioceptive motion signal may be sufficient for pursuit. Another far more commonly observed exception concerns images rendered stable with respect to the retina. Several investigators (HEDLUN and WHITE, 1959; RIGGS and TULUNAY, 1959; TEN DOESSCHATE, 1954) have shown that optically stabilized images may produce smooth oscillations of the eyes. After-images provide another example where smooth movements can be made without any moving visual target (MACK and BACHANT, 1969).

Why should stable images on the retina allow the release of pursuit eye movements? This poses a conceptual problem because, when done over a homogeneous or dark background, no retinal signal for motion can be present. What then is the stimulus for pursuit with a stabilized image? How can the pursuit movement begin?

One testable hypothesis concerns the "outflow" or "corollary discharge" model postulated to account for the stability of the visual world during eye movements (see, e.g. TEUBER, 1960). It is assumed that for voluntary eye movements, a corollary discharge is issued along with the efferent signal sent to the eye muscles so that the visual reafference resulting from the movement can be cancelled. Should there be a mismatch, then motion would be perceived, e.g. passively moving the eyeball by tapping it yields a motion signal because there is no corollary discharge to cancel the afference. This notion may also be applicable to the small fixational eye movements. BEELER (1967) has shown that during small involuntary fixational saccades there were visual threshold changes, perhaps reflecting the operation of a similar type of corollary discharge mechanism to the one postulated for gross eye movements. If so, then by having an image stable on the retina, any efferent signal issued to move the eye would remain *uncancelled* because no reafferent pattern could result that would correspond to the expected displacement of the retinal image. This uncancelled corollary discharge, therefore, could provide the initial internal motion signal that the oculomotor system would use to get the eye into pursuit.

The simple and obvious test of this uncancelled corollary discharge hypothesis is to monitor the miniature eye movement patterns while having a stabilized image (e.g. an after-image) present and seeing if a directional microsaccade always precedes the onset of pursuit.

PROCEDURE

The observer was seated in a dark room, his head steadied by a mouth-bite. With his left eye he fixated a mark on an illuminated horizontal scale and pressed a button which triggered

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a flash from a Multiblitz IIIb flash-unit which was masked to yield a uniform, circular after-image whose visual angle was approximately one degree. Fixation on different scale markings was used to place the after-images at various eccentricities in the horizontal retinal meridian.

As soon as the after-image was generated the scale illumination was extinguished and the observer turned his gaze to a 3-min red fixation light located in the median plane at a distance of 1 m and maintained fixation until the fixation light was extinguished by the experimenter. The observer then attempted to produce a smooth eye movement toward the eccentrically located after-image. After a short interval the experimenter turned on the fixation light for another trial. This sequence was continued as long as the after-image was clearly visible. When the after-image was difficult to see, the sequence ended and another after-image was generated. For observer D.P., in some sessions, the after-image was sustained by illuminating the background with a stroboscope flashing at about 10 Hz. No obvious differences were noted between eye movement records taken with and without the intermittent background illumination.

Horizontal eye position was continuously monitored by a contact-lens technique described in detail elsewhere (MATIN, 1964; MATIN and PEARCE, 1964). In this case, the method yielded measures precise to 1′ of arc over a range of 4°. The contact-lens, with a plane mirror imbedded in the temporal limbal area, was worn on the left eye; the right eye was occluded with a patch. The frequency response of the measurement system, limited by the Beckman Dynagraph used to provide permanent eye-movement records, was flat to approximately 90 Hz.

Both observers had normal extraocular muscle balance and appropriately corrected vision.

RESULTS AND DISCUSSION

The consistent and basic finding is that no microsaccade pattern precedes the onset of pursuit released by an after-image. In over 170 records we observed a microsaccade in the 0·5 sec period preceding the pursuit in less than 10 per cent of the cases. The microsaccade in those instances was as likely to be in the subsequent direction of pursuit as in the opposite direction. Thus, an uncancelled corollary discharge would not seem to be the source of the pursuit motion signal in this situation.

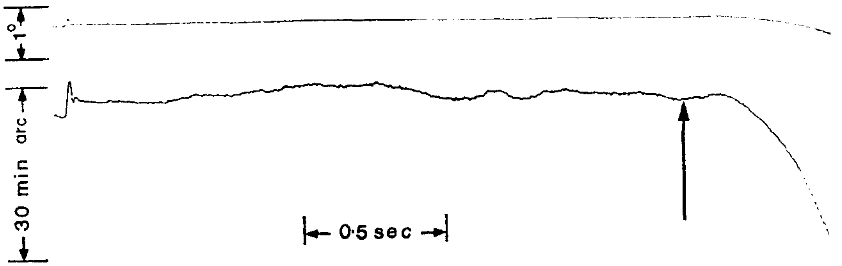

FIG. 1. DP pursuing right eccentric after-image. Both traces record the same eye movement, but the gain is approximately eight times greater in the lower trace. Arrow marks the offset of the fixation light.

A typical record, shown in Fig. 1, indicates that pursuit begins with a smooth transition of the drift into the higher velocity pursuit movement proper. In this instance DP pursued a 1° circular after-image located so that its left edge was just to the right of the point of fixation. The last microsaccade occurred more than 2 sec before the pursuit onset, and the latency for pursuit, measured from the time the fixation light was extinguished (indicated by an arrow on the record), is about 150 msec.

A characteristic feature of our records is the considerable diminution in microsaccade occurrence during fixation of the target when an after-image is present. This may indicate that with an after-image, subjects enter the "hold" fixation state described by STEINMAN, CUNITZ, TIMBERLAKE and HERMAN (1967). In this mode an observer does not actively strive to keep perfect fixation; rather he "rests" while keeping the direction of his gaze relatively constant.

Subjectively, it was noted by both of us that it was much easier to pursue to the right than it was to go to the left. This is consistent with measures of the latency for pursuit onset, measured from the time of extinguishing of the fixation light. Both M.S. and D.P. showed average latencies of around 130 msec when pursuing right eccentric after-images and of about 400–500 msec when pursuing left eccentric after-images. A directional preference is also manifest in our characteristic "signature" fixational eye movements made when actively fixing small stationary targets with no after-images present, i.e. we both show a tendency to drift more to the right than to the left. This may in fact indicate that an important aspect of getting an after-image to move involves the drift component of the fixational eye movement. This cannot be a complete explanation because the direction of pursuit is strongly coupled to the retinal locus of the after-image, i.e. we were unable to produce pursuit in other than the radial direction from the fovea to the after-image. Thus, with a left-eccentric after-image we could not go smoothly to the right and vice versa. Informal observations on other laboratory personnel shows this to be true in other quadrants. It could be considered adaptive in that the only eye movement possible is that which would (normally) be bringing the target image closer to the fovea.

It is possible that what we call drifts are in fact vergence movements and that "microvergences" are providing the motion signal for pursuit. We cannot exclude this experimentally for the few binocular records taken were not accurate enough to resolve microvergence. They did, however, clearly show the conjugate nature of the eye movements once started. If vergence eye movements were at the root of the smooth eye movements elicited using after-images, then you would expect large disjunctive eye movements to result. This does not happen. Additionally, the fact that one gets vertical pursuit with after-images located along the vertical retinal meridian would also seem to rule out the importance of vergences in starting the pursuit.

Eccentric after-images avoid the oscillations which can occur with foveally-centered after-images. On several occasions we recorded eye movements using foveal after-images and obtained records similar to those presented by TEN DOESSCHATE (1954), i.e. approximating sinusoids with a frequency of oscillation ranging from 0·5 to 1·0 Hz.

Figure 2 shows a few cycles of D.P.'s oscillatory eye movements with a 1° circular after-image centered on the fovea. The low gain record shows that the magnitude of the oscillation was about 1°; the range for the high gain record only allowed the left turn-around points to be measured. It is clear that changes in directions occur smoothly with no microsaccade pattern influencing the eye movement. M.S. provided similar records.

The degree of eccentricity of after-image placement (which varied from 0 to 2°) apparently did not influence the velocity of the pursuit. Wide ranges of pursuit velocities could be obtained from a *single* after-image locus. The velocity of pursuit is more likely to be related to

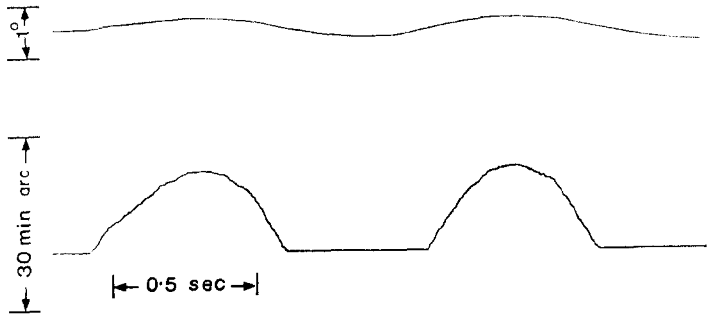

FIG. 2. Oscillations resulting from foveally centered after-image. High gain record on bottom shows only left turn-around points. D.P.

the salience of the after-image as something that the visual system can interpret as a target. Regrettably, an after-image is "stable" only in its position on the retina; it is dynamic in that it is always fading, changing hue, and waxing and waning in and out of prominance. The best records and highest velocities usually came after the generation of a fresh after-image.

In summary, our records show that pursuit eye movements elicited by after-images begin smoothly with no initiating microsaccade. Drift probably plays a significant role in pursuit initiation but, because the direction of pursuit is coupled to the retinal locus of the after-image, it cannot be the only determining factor.

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