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LETTER TO THE EDITORS

IMPAIRED MOTION DETECTION PRECEDING SMOOTH EYE MOVEMENTS[1]

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ONE OF the most intriguing notions in the study of brain function is the possibility that outgoing commands associated with intentional (motor) movements may internally influence or modify the perception of incoming sensory information. A classical illusion that seems to require such internal, sensory-motor interactions, is the apparent motion of an afterimage seen in the dark during a voluntary smooth movement of the eyes (HELMHOLTZ, 1910). Because the afterimage is stabilized on the retina, the apparent motion must be illusory. Presumably the illusion represents the effect of an internally initiated input correlated with the eye movement command (VON HOLST and MITTELSTAEDT, 1950), for no apparent motion is observed with passive movement of the eyeball. In order to strengthen the hypothesis that the illusory movement is associated with the intent to track a target, we sought to demonstrate that the afterimage appears to move before the onset of smooth eye movement.

METHOD

The subject, with his head positioned and held rigid by a bite-board, viewed the stimulus configuration shown in the inset of Fig. 1. This display was presented by a two-channel, Maxwellian view optical system described in detail elsewhere (RICHARDS, 1969). The background luminance was 20 cd/m^2. Superimposed upon the 11 deg background were two black lines 3 deg high that aided the subject in detecting movement of the test stimulus (an afterimage) and also provided a calibration for the eye-movement recording system. The latter was a phototransistor monitoring device devised by STARK, VOSSIUS and YOUNG (1962) which was capable of detecting 1/4 deg eye movements. In the middle of the background field in the region indicated by dotted lines, an intense bleaching light (5 log-trolands) could be presented, which created the afterimage whose motion the subject was instructed to detect.

Each experimental trial began with the subject fixating the central 1 × 3 deg region (dotted lines) for 4 sec while the bleaching light was on. Following the extinction of the bleaching light, the subject initiated an eye movement either to the left or to the right. (Our subject was unique in that he could initiate smooth eye movements in the absence of a moving stimulus.) Both saccades and smooth eye movements were studied, in a haphazard order. In each case the subject attempted to delay the onset of these movements by a fixed interval, which was in the neighborhood of one second. This brief interval allowed us to deliver an auditory probe (a click) after the formation of the after-image and yet well before the onset of the eye movement. The task of the subject was to report whether the click preceded or followed the appearance of motion of the afterimage. Thus, for any given trial, the actual temporal position of the click would be delayed by a timer set by the experimenter so that the click would be triggered before, near, or after the onset of the eye movement. Both the horizontal eye movements and the position of the click were plotted on a Moseley X–Y plotter, which gave the experimenter immediate feedback as to his success in choosing a delay that placed the click at the desired temporal position relative to the onset of the eye movement. Because the procedure was somewhat haphazard, being under the control of neither the subject nor the experimenter, it was necessary to pool the data into bins 30 msec wide as indicated in Fig. 1. The number of measurements obtained at each

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delay were distributed normally about −30 msec, with a peak of 13 trials; one standard deviation corresponded to 190 msec. Thus, in the region of −240 msec, approximately seven measurements were obtained.

RESULTS

Figure 1 summarizes the judgements made by RR as to whether the click preceded or followed the appearance of motion of the afterimage. When RR made saccades, only 5 per cent of the time did he indicate that the movement preceded the click when the auditory probe was delivered 120 msec before the onset of the saccade. Fifty per cent of the time, he judged the movement to appear at the onset of the saccade (somewhat surprising since the auditory and visual delays in the sensory pathways would not generally be expected to be equal). For the saccadic condition, the judgements may be fitted by a straight (dashed) line

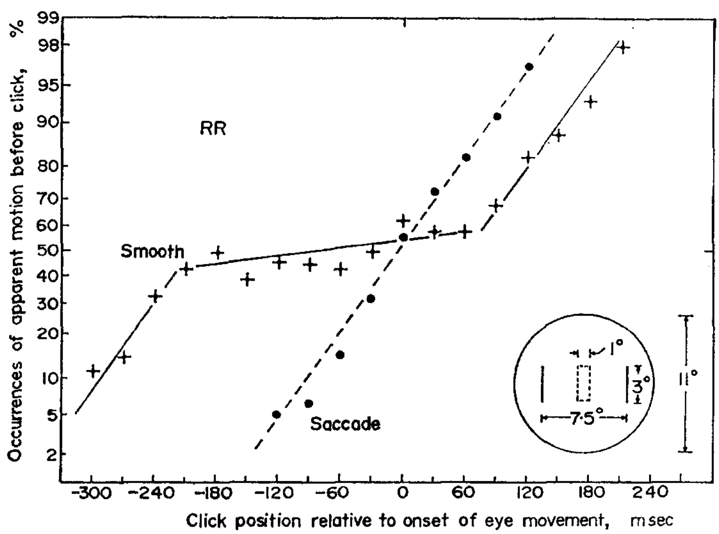

FIG. 1. Judgements of apparent motion of an afterimage at temporal positions preceding (−) and following (+) the onset of either a saccade (●) or a voluntary smooth eye movement (+). An auditory click serves to define the time at which the judgement is to be made. The inset shows the stimulus configuration.

that shows no indication of apparent motion preceding the onset of the saccade. Instead, the greatest value of these saccadic data is to provide an index of the variability of the judgements of the appearance of motion relative to the click.

An entirely different, and somewhat more complex result was obtained for the smooth eye movement condition. Up to 200 msec preceding the onset of the eye movement, RR was unable to provide a clear indication of whether or not apparent motion preceded the smooth eye movement. Over this region, approximately one half the judgements indicate motion preceding the eye movements, whereas the remaining half indicate no motion of the after-image. However, for temporal positions preceding the eye movement by more than 200 msec, RR's judgements are quite clear: there is no apparent motion this far in advance of the smooth eye movement.

DISCUSSION

For almost one-quarter of a second, mostly preceding the smooth eye movement, additional "noise" seems to be introduced when RR begins to initiate a voluntary smooth eye movement (average rate: 4 deg/sec). Between 210 msec before the onset of the smooth movement until 60 msec following the beginning of the movement, RR is unable to judge whether or not the afterimage appears to move. This impairment occurs only for the smooth and not for the saccadic eye movement, reinforcing the distinction between these two systems (RASHBASS, 1961).

Any definitive conclusions based upon only one subject must be guarded. RR is unique in that he belongs to only a small percentage of the population that can initiate voluntary smooth eye movements in the absence of a moving visual stimulus (STEINBACH, 1969; JORDON, 1970). By using such a subject, we avoid any possible confounding interference or masking effects related to the appearance of a stimulus for tracking that would move across the retina before the pursuit is initiated. Because this subject can initiate his own pursuit movement in the absence of any new visual input, the observed impairment in motion detection must be internally generated. The exact nature of the impairment is unclear, however. It could be due to a specific attenuation in either an egocentric or retinal signal for movement, or more simply it may be a non-specific consequence of a shift in attention from the afterimage to the volitional effort needed to initiate the smooth eye movement.

In order to extend our observation to a more typical subject, author WR attempted to train himself to make voluntary smooth movements also in the absence of a visual target. After several months, such smooth movements could be elicited at will, but somewhat erratically. When run on the above paradigm, WR's data for the saccadic condition were identical to those of RR shown in Fig. 1; on the other hand, for the smooth eye movement condition, the region of impaired motion detection was limited to 75 msec, beginning 60 msec before the eye movement. This interval is about twice the size of the region where small saccades (less than 15′) impair motion detection (BEELER, 1967). However, it is unlikely that small, spontaneous saccades are contributing to any portion of our result, for no such saccades are observed for periods extending well beyond 200 msec prior to the onset of pursuit eye movements elicited using afterimages (STEINBACH and PEARCE, in 1972).

Considering that smooth eye movements are generally associated with pursuit or tracking, our data suggest the possibility that motion information is suppressed prior to the initiation of a pursuit eye movement. Already, several electrophysiologists have reported excitability changes in the visual pathways that precede the onset of eye movements. (BIZZI, 1966; KAWAMURA and MARCHIAFAVA, 1968; STRASCHILL and HOFFMANN, 1970; WURTZ and GOLDBERG, 1971). More recently, SCHILLER and KÖRNER (1971) have found that single unit activity in the monkey colliculus may appear up to 400 msec preceding an eye movement, providing the subsequent eye movement is to a point in space that corresponds to the location of the unit's receptive field. Thus, in the monkey colliculus, whether or not unit activity appears prior to an eye movement depends upon the extent and direction of the subsequent eye movement. This result suggests that the observed psychophysical impairment of motion detection in man may not occur equally over the entire visual field. Instead, if impaired motion detection is a consequence of redirection of "attention" to another portion of the visual field, then movement detection may be impaired the most in the fovea and the least (or even enhanced) in the region of the subsequent target. However, an alternate interpretation may also apply to our paradigm: If our subject is detecting foveal motion by using peripheral cues as a reference (such as the outer limits of our visual field), then an impairment in peripheral movement detection could lead to our result. Perhaps this latter possibility is more likely considering that accurate pursuit requires good velocity sensitivity in the foveal region.[3]

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[3] A recent finding in monkey by WILSON and TOYNE (1970) suggests possible anatomical pathways for selectively differentiating between (foveal) pursuit and (more peripheral) saccadic systems in the superior colliculus.