porale. Handedness data were, for reasons beyond our control, not available to us. Since, however, about 93 percent of the adult population are right-handed, while 96 percent are left-brained for speech, our 100 cases must have consisted overwhelmingly of subjects that were left-brain dominant for speech. It would of course be most useful to study the patterns found in the brains of right-hemisphere-dominant subjects.

These studies support earlier assertions (*4–6*), in studies lacking quantitative data or based on small samples, that the supratemporal plane showed marked right-left asymmetries in man. Pfeifer (*5*) and von Economo and Horn (*6*) found by contrast no asymmetries in the same region in anthropoid apes.

While Heschl's gyrus contains the primary auditory cortex (*TC*) the planum temporale contains auditory association cortex (areas *TB* and *TA*) (*6*) which extends on to the lateral surface of the posterior portion of the first temporal gyrus. These regions of auditory association cortex on the left constitute the classical Wernicke's area, a region known from anatomical findings in aphasic patients (*7*) and from stimulation studies during neurosurgical procedures (*8*) to be of major importance in language functions. Our data show that this area is significantly larger on the left side, and the differences observed are easily of sufficient magnitude to be compatible with the known functional asymmetries (*9*).

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#### References and Notes

1. G. von Bonin, in *Interhemispheric Relations and Cerebral Dominance*, V. Mountcastle, Ed. (Johns Hopkins Press, Baltimore, Md., 1962), p. 1.
2. We thank Dr. T. McLardy and Dr. J. Segarra for making material available to us for study.
3. C. J. Connolly, *External Morphology of the Primate Brain* (Thomas, Springfield, Ill., 1950), pp. 144 and 205.
4. P. Flechsig, *Neurol. Zentralbl.* **27**, 2, 50 (1908).
5. R. A. Pfeifer, in *Handbuch der Neurologie*, O. Bumke and O. Foerster, Eds., (Springer, Berlin, 1936), vol. 6, p. 533.
6. C. von Economo and L. Horn, *Z. Ges. Neurol. Psychiat.* **130**, 678 (1930).
7. O. Zangwill, in *Handbook of Physiology*, sect. 1, "Neurophysiology" (Williams and Wilkins, Baltimore, Md., 1960), vol. 3, p. 1709; A. Meyer, in *Collected Papers of Adolf Meyer*, E. Winters, Ed. (Johns Hopkins Press, Baltimore, Md., 1950), vol. 1, p. 358.
8. W. Penfield and L. Roberts, *Speech and Brain-Mechanisms* (Princeton Univ. Press, Princeton, N.J., 1959), p. 130.
9. Some of the work was carried out at the Boston Veterans Administration Hospital. Supported in part by grant NB-06209 from the U.S. Public Health Service.

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# Eye Tracking of Observer-Generated Target Movements

Abstract. *When an observer moves his arm he shows more precise visual tracking of a target mounted on his fingertip—the eye lags behind the target less and makes fewer corrective saccades—than when he relaxes his arm and the experimenter moves it in a similar manner. Apparently the control system for eye movements can use outflow (efferent) signals in order to anticipate motion of the self-moved target.*

When an observer attempts to keep his line of sight fixed on a moving target, his eyes perform tracking movements. The eye can remain on target with little or no lag when the target moves periodically at a low frequency (*1, 2*). If motion of the target is made aperiodic, its "predictability" decreases and tracking performance deteriorates, as indicated by increasing lag between orientation of the eye and direction of target. These results have been found with targets that move independently of control by the observer. The tracking of targets that are moved by the observer himself has not hitherto been examined, although one might expect that any additional information about target motion would aid tracking. We now report results indicating that the observer can more accurately track a target that he moves himself than a target that is moved without his control.

In order to compare the accuracy of tracking self-produced target motion with that of independent motion, the observer tracked a spot on his own finger under two conditions: (i) when he himself moved his arm in an irregular manner (hereafter called the active condition), and (ii) when his relaxed arm was moved in a similar manner by an external force (passive condition). The movements of both eye and target were recorded during the two conditions of target motion. In both cases, the displacements and rates of movement of the arm were comparable, but only in the case of observer-produced movement was there additional information available and potentially useful to the oculomotor control system for tracking, namely the efferent or outflow signals to the musculature present with all voluntary movements (*3*).

The target was a 2-mm square of black tape fastened on the fingernail of the third finger of the right hand of the observer. His right arm rested on a flat lever, pivoted near the elbow, restricting movement of the target to an arc in a frontal plane 30.5 cm from the cornea of the right eye. Movement of the target was limited to 10 degrees (in visual angle) to the right and left of the observer's midsagittal plane. Registration of arm (and therefore target) position was provided by a potentiometer geared to the pivot of the lever. Horizontal eye movements were recorded using a photoelectric technique yielding measurements accurate, in this instance, to one-half degree of horizontal displacement of the eye (*2*). The observer's head was held in position by having him bite a bar holding a wax dental impression. Although he viewed his right hand binocularly, the horizontal movements of only the right eye were recorded.

Four male and two female students and employees at Massachusetts Institute of Technology were used as observers in the study. Their ages ranged from 19 to 33 years. The visual acuity of all observers was sufficient to perform the task without corrective lenses. In the active condition, the observer was instructed to look at the black square of tape on his fingertip and to follow it as best he could while rapidly moving his hand back and forth at an irregular rate of approximately three to four reversals of direction per second within the 20-degree range of travel of the lever. In the passive condition, the observer relaxed his arm on the lever, allowing the experimenter to move the arm through a pattern of displacements similar to the one the observer used in the active condition. The observer was again instructed to look at the target at all times. Arm (target) position and eye position were recorded simultaneously on two channels of a Sanborn recorder, operating at a paper speed of 100 mm/sec. Only the data from observers whose movements in the active condition were very similar to their movements in the passive condition (determined by counting the number of direction reversals and checking average amplitude during the first 15 seconds of recording) were kept for analysis.

Figure 1 shows a typical record of hand and eye movements under active and passive conditions. For each condition the target (hand) record is on top, and maximum peak-to-trough

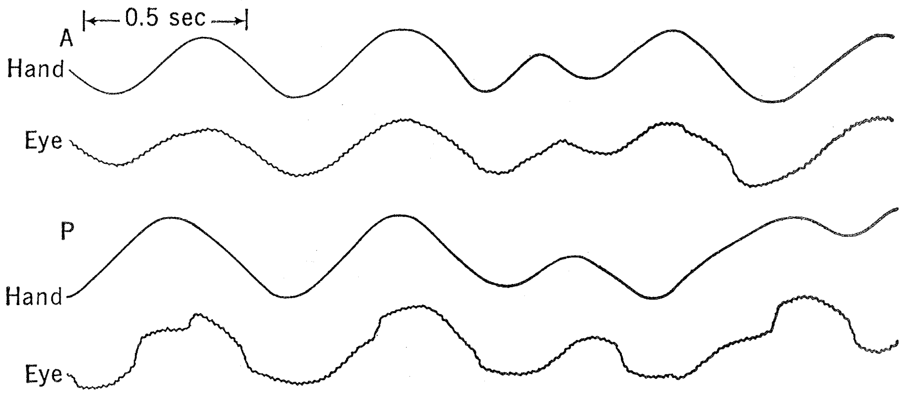


Fig. 1. Eye- and hand-movement records for active (*A*) and passive (*P*) conditions of hand (target) movement. Read time from left to right. The ripple present in the eye-movement records is background noise (60 cycle/sec).

travel represents 20 degrees of visual angle. The record for the active condition shows that the eye followed the target rather closely. For this observer, the mean lag between eye and hand for reversals of direction of motion approximates zero. Even though the target is moving quite rapidly (up to five reversals per second), the eye tends to stay on target. The passive record shows an obvious qualitative difference. This record, not nearly as smooth as that from the active condition, is characterized by a large number of saccades. As judged by positions of peaks and troughs, the eye appears to lag behind the hand much more often than in the active condition. The amount of lag could not be determined precisely because the shape of the trace was often obscured by the saccades, making it difficult to define the peaks and troughs from which the lag could be calculated.

Because of the uncertainty in defining the lag and also because the measurements of absolute eye position can vary slightly within any given session (*4*), the analysis was carried out at a simpler level. The number of saccades was taken as the measure of tracking accuracy. If a target is tracked perfectly, its image remains "locked" onto the fovea and the movements of the eye precisely match those of the target. However, as the target moves off the fovea, an increasing positional error between target and fovea will make a corrective saccade necessary to reposition the fovea on the target image.

Table 1. Numbers of saccades occurring during first 15 seconds of tracking.

| Subject | Fingertip target moved | |
|---|---|---|
| | Actively | Passively |
| K.W. | 39 | 75 |
| D.M. | 38 | 68 |
| M.S. | 4 | 33 |
| E.B. | 9 | 32 |
| P.S. | 38 | 65 |
| I.P. | 40 | 60 |
| | *Averages* 28.0 | 55.5 |

The numbers of saccades occurring in the first 15 seconds of tracking under the active and passive conditions are presented in Table 1. The mean number of saccades in the active condition for the six subjects was 28.0, with individual differences evident. In the passive condition, the mean increased to 55.5 and the increase occurred for all observers. This difference was found to be significant at $P < .001$ according to a *t*-test for correlated means. The ability of the eye to remain on target, then, is enhanced when the movement of the target is produced by the observer.

In order to assess a possible contribution of the passively moved arm to tracking performance, an additional condition was included. Four observers tracked a 2-mm square of black tape fixed on the lever in a position corresponding to the former position of the fingertip when the observer's arm had rested on the lever. The experimenter then moved the lever in the same manner as in the passive condition. The eye-movement records for this type of target motion were very similar to those obtained when the target was on the fingertip and the arm was moved passively. A count of saccades in the first 15 seconds showed no significant difference between the numbers of saccades in the passive and target-only conditions.

This investigation has demonstrated that tracking is improved when the target is a part of the observer and is moved by himself. This improvement is evident from the fact that the eye smoothly followed irregular movements of the target that approached or exceeded four reversals per second. There is considerable evidence that at frequencies approaching 2 cycle/sec the accuracy of tracking a predictable (sine wave) stimulus has already fallen off (*1*, *2*). It is all the more surprising that with a target moving so rapidly and irregularly the eye can still follow with smooth movements and with relatively few corrective saccades. That this enhanced tracking performance results from use of efferent signals is supported by the differences that are found between the active and passive conditions.

These findings support the view that the efferent signals responsible for moving the arm also provide information about target motion that is used by the system that controls tracking movements of the eye. These results are hardly surprising from a teleological (that is, evolutionary) point of view, since the ability to keep the image of a manipulated object on the area of sharpest vision on the retina is highly adaptive.


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**References and Notes**


1. G. Westheimer, *AMA Arch. Ophthal.* **52**, 932 (1954); P. J. Dallos and R. W. Jones, *Inst. Electrical Electron. Eng. Trans. Automat. Contr.* **AC-8**, 218 (1963); J. A. Michael and G. Melvill Jones, *Vision Res.* **6**, 707 (1966); D. H. Fender, *Symp. Soc. Exp. Biol.* **18**, 401 (1964).
2. L. Stark, G. Vossius, L. R. Young, *Inst. Radio Eng. Trans. Human Factors Electron.* **HFE-3**, 52 (1962).
3. Several authors have considered the use of internally monitored efferent signals for maintaining stability of the visual world during eye movements. For a summary of these notions see H.-L. Teuber's discussion of corollary discharge in *Handbook of Physiology*, J. Field, H. W. Magoun, V. E. Hall, Eds., sect. 1, "Neurophysiology" (Williams and Wilkins, Baltimore, Md., 1960), vol. 3, pp. 1647–1648.
4. The photoelectric recording technique has several sources of inaccuracy. Reflection of light is altered when the corneal surface dries slightly between blinks, thereby changing the output of the recorded signal (J. Krauskopf, V. Graf, K. Gaarder, *Amer. J. Psychol.* **79**, 73 (1966). The setup used in this study was sensitive to head movement which was considerably reduced by using the bite bar and a forehead rest, but not altogether eliminated. Finally, if the observer squinted or moved his eyelids, the output was altered.


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