Notes and Comment

Impressions of visual direction from extraocular afference

WAYNE HERSHBERGER

Northern Illinois University, DeKalb, Illinois

It is common knowledge that pressing upon the side of one's eye with a finger creates an impression of movement of the visible environment. Stark and Bridgeman (1983) have noted that such is the case even when the eye maintains fixation of a visible target throughout the eye-press. Hence, they conclude that the impression is extraretinal in origin, and claim, further, that this extraretinal signal is simply the corollary discharge of a compensatory efference that serves to offset the disturbance to fixation provided by the finger. Were this the whole truth, the eye-press and the apparent motion to which it gives rise would always be out of phase: whenever the eye-press was to the right, the apparent motion would be to the left, and vice versa. This, however, is not the case. The direction of apparent motion to which an eye-press gives rise is gaze dependent.

When an eye is deviated from its primary position, as in the fixation of an eccentric target, pressing the eyeball as if to rotate it back toward its primary position yields an impression of environmental motion opposite in direction to the eye-press. However, pressing the eyeball as if to rotate it even farther from its primary position yields an apparent motion in the same direction as the eye-press. The reader is invited to verify this for himself/herself.

With one eye, say your left, fixate an eccentric target situated about 30 deg to your left and gently press your eye to the right with an oscillating series of nudges. The visible target will appear to move to the left, oscillating 180 deg out of phase with the nudges. With the eye maintained in its primary position, fixating a target located straight ahead, the same phase relationship obtains (Stark & Bridgeman, 1983). However, repeat the procedure (same eye, same nudges) while fixating a target situated about 30 deg to your right. The target will appear to move to the right, oscillating in phase with the nudges.

This in-phase relationship has univocal theoretical implications, because it can be attributed neither to retinal motion of the target's image nor to a corollary discharge of compensatory oculomotor efference: the apparent motion that would stem from either of these two sources would be 180 deg out of phase with

the eye-press. The apparent motion that is in phase with the eye-press must, therefore, be a perceptual manifestation of extraocular afference, the only potential source remaining.

Incredible as it may seem, this simple observation, so readily at hand, appears to provide the best, albeit belated, evidence that the extraocular stretch receptors influence the perception of visual direction. Although Sherrington (1918) championed such a notion 65 years ago, the evidence accumulated in the meantime has been arguably thin (Matin, 1972, 1982; Roland, 1978; Shebilske, 1977). Previous evidence has been basically of one of two types, both of which are indirect: (1) the static appearance of the normally visible environment when one attempts to move the fully paralyzed eye (Brindley, Goodwin, Kulikowski, & Leighton, 1975; Siebeck, 1954; Stevens, Emerson, Gerstein, Kallos, Neufeld, Nichols, & Rosenquist, 1976), or (2) the detection and compensation for unintended eye positions (Shebilske, 1976; Skavenski, 1971, 1972; Skavenski & Steinman, 1970). The former type of evidence appears to demonstrate that sensed efference does not alone determine the perceived direction of visible targets; hence, extraocular afference is implicated. However, this evidence is compromised by what Stark and Bridgeman (1983) have called VCM, the visual capture of Matin. Matin, Picoult, Stevens, Edwards, Young, and MacArthur (1982) have shown that a well-illuminated visual field serves to mask some of the perceptual effects of partial paralysis and suggest that it may similarly influence the effects of full paralysis as well. That is, although a single stationary spot of light in the dark appears to move about when one attempts to move one's partially paralyzed eyes, subjects attempting to look about a well-illuminated room fail to note any change in the direction of a target judged to be straight ahead, irrespective of whether they are partially or fully paralyzed (cf. Harris, 1974; Rock, Goldberg, & Mack, 1966; Welch, 1978). Hence, Matin et al. (1982) have concluded "that it will now be necessary to reexamine the total paralysis situation in darkness . . . to decide on the source of EEPI (extraretinal eye position information]" (p. 200).

The second type of evidence, although less tenuous, is also less direct, because it demonstrates only that extraocular afference influences sensed eye orientation, not perceived target direction. Skavenski's (1971, 1972; Skavenski & Steinman, 1970) research has shown that extraocular afference is utilized in the dark to detect and compensate for departures from a preintended direction of gaze, and Shebilske's (1976) research has implicated extraocular afference in the

The author's mailing address is: Department of Psychology, Northern Illinois University, DeKalb, IL 60115.

detection and compensation for dysmetric saccades. However, "there are almost certainly differences between the sensory processes leading to perception and those leading to saccadic eye movements" (Hallet & Lightstone, 1976b, p. 99), for, although a fixation target flashed during a saccade "elicits a subsequent goal-directed saccade of normal amplitude and appropriate latency" (Hallet & Lightstone, 1976a, p. 107), a stimulus flashed in darkness during a saccadic eye movement tends to be perceptually mislocalized (Matin, 1972, 1982; Matin & Pearce, 1965). Hence, this type of evidence is, at best, indirect.

The best direct evidence of the influence of extraocular afference upon the perception of visual direction appears to be the observation reported here: the illusory, in-phase displacement of the visual field that accompanies a simple eye-press. Of course, since the observed phase relationship between the displacements of the eye and the visual environment depend upon the general direction of gaze, the simple eye-press experiment may be said to implicate both afferent and efferent factors, with the observed phase relationship serving as an index of their relative influence for a given direction of regard. It is not clear why the relative influence of these two factors should depend upon the direction of regard. It is only clear that it does. (It is almost as if the extraretinal contribution to the perception of visual direction were a hybrid signal comprising the efference sent exclusively to contracting extraocular muscles combined with the afference sent exclusively from those agonists' respective antagonists; cf. Matin, 1982.)

Previous research (Skavenski, Haddad, & Steinman, 1972) had seemed to show that the visual displacement to which an eye-press gives rise is gaze independent. Skavenski et al. had subjects fixate a red light in the dark while the eye was tugged to the right or left by a weighted string pulling upon a lever attached to a tightly fitting scleral contact lens. When, simultaneously, the subject adjusted the position of a second, white light so that it appeared to be straight ahead, he always shifted it away from the objective straight ahead in a direction *opposite* to the eye displacement, and did so irrespective of whether the red fixation target was located straight ahead or eccentrically to his right. That is, the visual displacement to which the eyepull gave rise was independent of the direction of regard: even with the gaze deviated to the right, pulling the eye to the right displaced the visual field to the left. However, the generality of these findings by Skavenski et al. is severely limited by the fact that their eccentric target's location deviated the subject's gaze only 13.5 deg from the eye's primary position. Had the location of the red fixation target been more eccentric, they surely would have found that the direction of visual displacement

to which an eyepull gives rise is ultimately dependent upon the eye's general direction of regard.

REFERENCES

- BRINDLEY, G., GOODWIN, G., KULIKOWSKI, J., & LEIGHTON, D. (1975). Stability of vision with a paralyzed eye. *Journal of Physiology* (London), **253**, 65-66.
- HALLET, P. E., & LIGHTSTONE, A. D. (1976a). Saccadic eye movements to flashed targets. *Vision Research*, **16**, 107-114.
- HALLET, P. E., & LIGHTSTONE, A. D. (1976b). Saccadic eye movements towards stimuli triggered by prior saccades. *Vision Research*, **16**, 99-106.
- HARRIS, C. S. (1974). Beware of the straight-ahead shift—a non-perceptual change in experiments on adaptation to displaced vision. *Perception*, **3**, 461-476.
- MATIN, L. (1972). Eye movements and perceived visual direction. In D. Jameson & L. Hurvich (Eds.), *Handbook of sensory physiology* (Vol. 7). Heidelberg: Springer-Verlag.
- MATIN, L. (1982). Visual localization and eye movements. In W. A. Wagenaar, A. H. Wertheim, & H. W. Liebowitz (Eds.), *Symposium on the study of motion perception*. New York: Plenum.
- MATIN, L., & PEARCE, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science*, **148**, 1485-1488.
- MATIN, L., PICOULT, E., STEVENS, J. K., EDWARDS, M. W., YOUNG, D., & MACARTHUR, R. (1982). Oculoparalytic illusion: Visual-field dependent spatial mislocalizations by humans partially paralyzed with curare. *Science*, **216**, 198-201.
- ROCK, I., GOLDBERG, J., & MACK, A. (1966). Immediate correction and adaptation based on viewing a prismatically displaced scene. *Perception & Psychophysics*, **1**, 351-354.
- ROLAND, P. E. (1978). Sensory feedback to the cerebral cortex during voluntary movement in man. *Behavioral and Brain Sciences*, **1**, 129-171.
- SHEBILSKIE, W. L. (1976). Extraretinal information in corrective saccades and inflow vs. outflow theories of visual direction constancy. *Vision Research*, **16**, 621-628.
- SHEBILSKIE, W. L. (1977). Visuomotor coordination in visual direction and position. In W. Epstein (Ed.), *Stability and constancy in visual perception*. New York: Wiley.
- SHERRINGTON, C. S. (1918). Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain*, **41**, 332-345.
- SIEBECK, R. (1954). Wahrnehmungsstörung und Störungswahrnehmung bei Augenmuskellähmungen. *Von Graefes Archiv für Ophthalmologie*, **155**, 26-34.
- SKAVENSKI, A. A. (1971). Extraretinal correction and memory for target position. *Vision Research*, **11**, 743-746.
- SKAVENSKI, A. A. (1972). Inflow as a source of extraretinal eye position information. *Vision Research*, **12**, 221-229.
- SKAVENSKI, A. A., HADDAD, G., & STEINMAN, R. M. (1972). The extraretinal signal for the visual perception of direction. *Perception & Psychophysics*, **11**, 287-290.
- SKAVENSKI, A. A., & STEINMAN, R. M. (1970). Control of eye position in the dark. *Vision Research*, **10**, 193-203.
- STARK, L., & BRIDGEMAN, B. (1983). Role of corollary discharge in space constancy. *Perception & Psychophysics*, **34**, 371-380.
- STEVENS, J. K., EMERSON, R. C., GERSTEIN, G. L., KALLOS, T., NEUFELD, G. R., NICHOLS, C. W., & ROSENQUIST, A. C. (1976). Paralysis of the awake human: Visual perceptions. *Vision Research*, **16**, 93-98.
- WELCH, R. B. (1978). *Perceptual modification*. New York: Academic Press.

(Manuscript received January 27, 1984;
accepted for publication February 6, 1984.)