

The extraretinal signal for the visual perception of direction*

ALEXANDER A. SKAVENSKI†, GENEVIEVE HADDAD
and ROBERT M. STEINMAN

University of Maryland, College Park, Maryland 20742

The dependence of the perception of direction on two kinds of extraretinal signals was measured by asking Ss to indicate the position of a fixation target relative to the subjective straight ahead. Outflow was studied by making such localizations while the fixating eye was loaded by means of weights attached to a suction contact lens. Inflow was studied by making such localizations with brief test flashes to a passively rotated eye while the other eye fixated. Shifts in the perceived direction of the fixation target were in line with predictions from outflow theory and not influenced by conflicting inflow signals.

We can accurately perceive where an object is located and whether it is moving, despite changes in the orientation of our eye. The veridicality of these percepts cannot be explained solely on the basis of retinal information: some type of nonvisual (extraretinal) eye position information must be involved (Matin, Matin, & Pearce, 1969). Two sources have been proposed: Helmholtz (1866) maintained that our knowledge of eye position derives from the commands sent to the extraocular muscles (outflow), while Sherrington (1918) maintained that such knowledge is produced by stretch receptors in the extraocular muscles (inflow).

Currently, Helmholtz's theory is widely accepted. Support comes from Helmholtz's (1866) observations (confirmed by Brindley & Merton, 1960; Irvine & Ludwig, 1936; Kornmüller, 1931) that when the eye is passively displaced, the target rather than the eye is perceived to have moved. And, when the eye is restrained during an attempted eye movement, the target is perceived to have moved in the direction of the attempted but not executed eye movement. These observations suggest that eye position compensation depends largely on outflow. The contribution of inflow cannot be ruled out, however, because relationships between perceived shifts in target direction and changes in extraretinal eye position information have not been measured. We decided to make

such measurements because Skavenski (1972) showed that an inflow signal can be used to control eye position. Perhaps this signal also contributes to the perception of direction?

METHOD

Subjects

Two of us (R.S. and A.S.) participated in these experiments. Both had considerable prior experience in making psychophysical observations and also in using retinal signals (e.g., Puckett & Steinman, 1969; Steinman, Cunitz, Timberlake, & Herman, 1967) and extraretinal signals (e.g., Skavenski & Steinman, 1970; Skavenski, 1971) to control eye position. Both were emmetropic. R.S. had 2.5 diopters esophoria and A.S. 3 diopters exophoria by the Maddox Patch Cover Test.

Apparatus and Procedure

Horizontal eye positions were recorded by means of a diffuse reflection technique, viz, a photoresistor measured the amount of diffuse infrared light ($9,000 \text{ Å} \pm 40$) reflected from the limbus (where the white sclera joins the dark iris). With suitable calibration and linearizing procedures, horizontal eye position could be measured to less than $\frac{1}{4}$ deg of arc over a 16-deg arc range. Head position was stabilized by an acrylic dental impression bite board.

We can determine whether the perception of direction depends on inflow or outflow by manipulating both sources separately while measuring the perceived direction of a fixation target. Disruption of the normal correspondence between inflow and outflow was accomplished by applying loads to S's right eye by means of a tightly fitted molded scleral contact lens. These lenses were held firmly in place by suction (28-31 mm of mercury), permitting application of large forces to the eye without lens slippage. A 3-cm stalk

was cemented to the contact lens and weights (located to the left or right of the eye) were attached to the stalk by means of threads that passed over Teflon pulleys. Thus, if a weight was added to the thread on S's left, its downward pull would apply a leftward force on his eye (see Skavenski, 1972, for a photograph of the loading arrangements).

Prior to the experiments, we obtained estimates of the variability of each S's subjective straight ahead (the direction referenced by the midsagittal plane passing through his body) by using an adjustment method in which S placed a movable 20-min arc diameter tungsten white-light target (luminance, $1.5 \log \text{ mL}$) on the imagined line connecting his belly button to his Adam's apple. The S moved the white test target along a horizontal perimeter by pulling on a nylon loop that changed the test target's horizontal orientation relative to his subjective straight ahead. Measurements were made with S seated in a totally dark cubicle. The E moved the test target to some eccentric position and then switched it on. The S then adjusted its position until he was satisfied that he had placed it straight ahead. Left and right starting positions were alternated, and initial test target displacements were varied haphazardly. Ten measurements of the subjective straight ahead were also made prior to each experimental session. These measurements were used to position a red fixation target (described below).

Two experiments were performed. In the first, shifts in the perceived direction of the fixation target were measured while outflow was systematically varied (inflow constant). In this experiment, S fixated a 14-min arc diameter red target (luminance, $1.45 \log \text{ mL}$) presented either straight ahead or 13.5 deg of arc to his right. The target was seen only by the right eye—the left eye was covered and closed. Measurements of perceived direction were made under six loading conditions: 4.5, 7.2, or 9.0 g applied to the left or right. Measurements were also made when no load was applied.¹ Trials began when E signaled that loading was complete. The E then moved the white test target to a haphazardly selected starting position and switched it on. The S then moved the white test target until he was satisfied that it was straight ahead. The S kept his line of sight near the red fixation target throughout the entire trial (eye position was monitored).

The logic of this experiment is as follows: As long as S continues to fixate the red target, inflow from the extraocular muscles remains constant. He must change the outflow signal to

*Supported by Grant EY325 from the National Eye Institute. Address reprint requests to R. M. Steinman, Department of Psychology, University of Maryland, College Park, Maryland 20742. The authors thank Dr. David A. Robinson for his helpful criticisms and suggestions. Most of the information contained in this paper was reported at the A.R.V.O. meeting of April 1971 at Sarasota, Florida.

†Now at the School of Medicine, Department of Biomedical Engineering, The Johns Hopkins University, Baltimore, Maryland 21205.

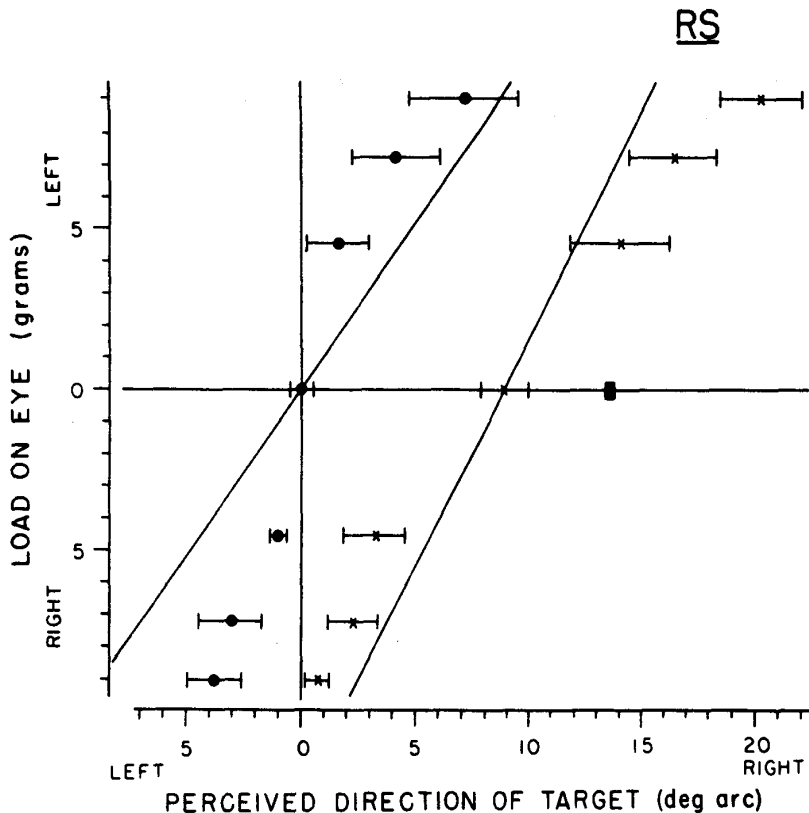


Fig. 1. Mean shifts in the perceived direction of a fixation target for various loads applied to the left and right of S.R.S.'s right eye. R.S.'s mean straight-ahead position (based on trials when no load was applied) is shown as the intersection of the axes. Mean shifts in perceived direction are plotted as circles when the fixation target was presented straight ahead and as crosses when the target was presented 13.5 deg of arc to the right. The rectangle on the right shows the objective position of the displaced fixation target. Oblique lines show the perceived shift in target direction predicted from outflow theory. Each data point is the mean of 10 position measures. Error bars show one standard deviation on each side of the means. The subjective straight-ahead was found to be biased towards the fixation target when the fixation target was presented 13.5 deg of arc to the right. We cannot tell from the present experiments whether or not this constant error represents a compression of the subjective representation of space.

his extraocular muscles, however, to keep his eye in the same orientation after the load is applied. The innervation pattern required to maintain the line of sight when the eye is loaded, however, normally rotates the unencumbered eye to a different position. For example, if a spring constant of 1.25 g/deg (Robinson, 1964) is assumed and a load of 10 g is applied to the right, then S must increase the tension on his medial rectus muscle by 10 g to continue fixating a target. Such a change in the innervation pattern would normally rotate S's unencumbered eye to the left by about 8 deg of arc.

Ten measurements (five rights and five lefts) were made for each S under each loading condition with the red fixation target straight ahead. The order of the loads was randomized:

directions were alternated. The procedure was then repeated with the red fixation target 13.5 deg of arc to the right of Ss' straight ahead.

In the second experiment, shifts in the perceived direction of the fixation target were measured while inflow was systematically varied (outflow constant). Two pairs of plane polarizers were arranged so that S could see only the red fixation target with his unencumbered left eye and see only the white movable test target with his loaded right eye. The S fixated the red target for 2.65 sec. The fixation target was then turned off for 125 msec, during which time the movable white test target appeared. The red fixation target reappeared immediately thereafter. The S then moved the test target carrier so that the small white test light would appear

nearer to his straight ahead when it was turned on, briefly, 2.65 sec later. This procedure continued until S was satisfied that the flashing white test light was located straight ahead.

Since the two eyes are yoked very well, fixation of the red target with the left eye maintains a constant innervation pattern to both eyes. Inflow from the right eye can be varied, however, by application of loads that cause the eye to rotate passively when it is *not* provided with a fixation target.³ Measurements were made with the red fixation target (seen only by the left eye) 13.5 deg of arc to the right for R.S. and straight ahead for A.S. Twelve left loads of 7.2 g and 12 of 9.0 g were applied to the right eye of S.R.S. Twenty right loads of the same magnitude were applied to the right eye of S.A.S. The same number of measurements were made for each S when no load was applied.

Oculomotor spring constants for the loads used in the present experiments were measured by Robinson's (1964) technique. Robinson measures spring constants by a technique similar to the procedure used in the second experiment, except that the right eye never has any visual input and rotations produced by the various loads are measured with an eye position monitor.

RESULTS AND DISCUSSION

The S's ability to locate his subjective straight ahead proved to be reasonably consistent, making it possible to use this subjective reference direction to measure relatively small changes in the perceived direction of the fixation target. Mean subjective straight-ahead positions did not differ much from session to session (range = 1.6 deg of arc). Measures made within each session varied less.

Perceived Direction Depends On Outflow When Inflow Is Constant

The mean shift in the perceived direction of the fixation target as a function of load was calculated by finding the difference between the mean straight-ahead position when no load was applied to the eye and the mean straight-ahead position when a load was applied to the eye. These data are summarized in Fig. 1 for S.R.S. and in Fig. 2. for S.A.S. Perceived shifts in the direction of the fixation target that would be predicted from outflow theory are also shown for both fixation target positions (oblique lines). These predicted lines are based on measured spring constants: 1.0 (SD = 0.2) g/deg and 1.5 (SD = 0.4) g/deg for R.S. fixating the straight-ahead (0) and the right 13.5-deg-arc fixation target, respectively. A.S.'s spring constants were 1.3 (SD = 0.4) g/deg and 1.1

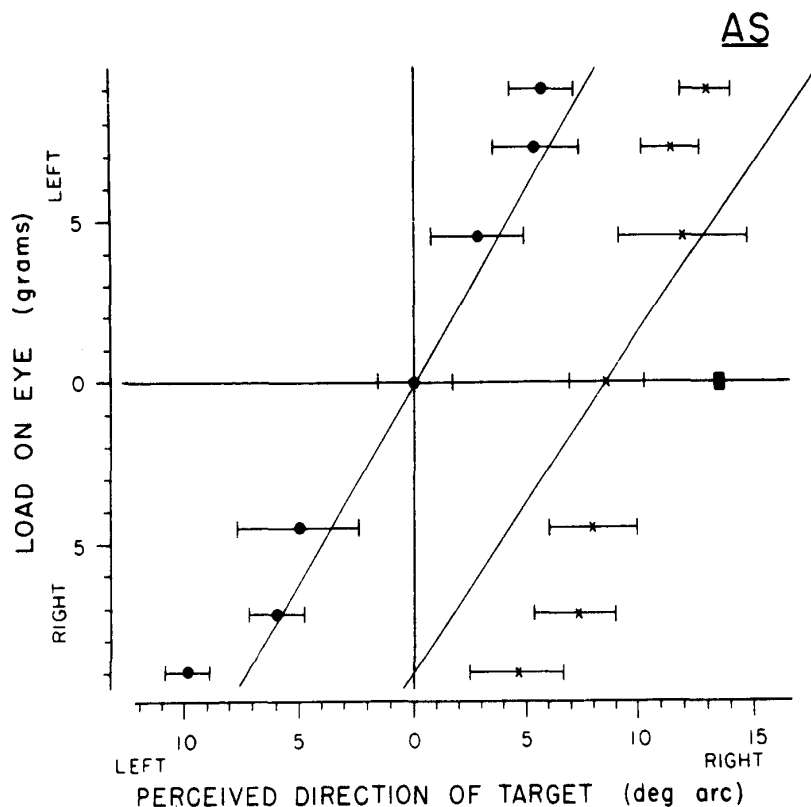


Fig. 2. Mean shifts in the perceived direction of a fixation target for various loads applied to the left and right of S.A.S.'s right eye. A.S.'s mean straight-ahead position (based on trials when no load was applied) is shown as the intersection of the axes. Mean shifts in perceived direction are plotted as circles when the fixation target was presented straight ahead and as crosses when the target was presented 13.5 deg of arc to the right. The rectangle on the right shows the objective position of the displaced fixation target. Oblique lines indicate the perceived shift in target direction predicted from outflow theory. Each data point is the mean of 10 position measures. Error bars show one standard deviation on each side of the means.

(SD = 0.5) g/deg at the same target positions.

Outflow prediction lines have the following significance. The slopes of the oblique lines for each S are equal to his measured spring constants. The zero intercepts are plotted through the positions measured when no load was applied to the fixating eye. Thus, if Ss based their direction judgments on outflow, the fixation target would be perceived to shift in a direction opposite to the applied load by an amount equal to the applied load times the reciprocal of the spring constant. If, however, Ss based their judgments of the fixation target direction only on inflow information, there would be no shift in perceived direction and the data points would fall on vertical lines near 0 and 13.5 deg of arc to the right. Figures 1 and 2 show that this was not the case: perceived direction varied when oculomotor outflow changed and inflow was kept constant. The direction in which the fixation target

shifted depended on the direction of load application (the fixation target moved opposite to the side on which the load was applied). Increasing the load produced monotonic increases in the size of the shift for R.S. and almost monotonic shifts for A.S. (there was one exception). These measures show that, to a first approximation, perception of direction is directly proportional to the magnitude of the outflow signal.

Although many data points do not fall on the outflow prediction lines, we do not feel that these data provide convincing evidence for an inflow contribution to perceived direction because the departures from the outflow prediction do not consistently favor inflow. That is, the data points do not always deviate towards a vertical line passing through the no-load position, viz, R.S.'s right loads while fixating the 13.5-deg-arc target position and A.S.'s right loads with the fixation target located straight ahead. This interpretation is supported by the

results of the next experiment as well as some subjective observations described below.

Perceived Direction Does Not Depend On Inflow When Outflow Is Constant

Figure 3 shows the mean perceived direction of the red fixation target when the red fixation target was seen by the left eye and the white test target was seen briefly by the right eye. We assume that the outflow to both eyes is determined by the eye (left) that fixates the red target which is visible almost continually. The right eye does not see the red fixation target and will, therefore, rotate passively when a load is applied (our eye position monitor confirmed this expectation). Such passive rotations change the eye position information flowing into the oculomotor system. If only outflow is important, the perceived direction of the red fixation target (seen only by the left eye) will not change when a load is applied to the right eye. Allowance must be made (1) for the constant error introduced by the passive rotation of the right eye which shifts the retinal locus that corresponds to the subjective straight ahead and (2) for Ss' phoria. The former was done by subtracting the amount of passive rotation of the right eye from the mean subjective straight ahead measured with this eye and the latter by adding R.S.'s esophoria to and subtracting A.S.'s exophoria from the mean perceived direction of the red fixation target. If, on the other hand, the perception of direction of the red fixation target is influenced by oculomotor inflow from the passively rotated right eye, the data points would not fall on vertical lines near 0 deg of arc for A.S. and right 13.5 deg of arc for R.S.

As can be seen in Fig. 3, the perceived direction of the red fixation target depended primarily on outflow: A.S.'s data points fall almost vertically. R.S.'s data were not as close to the vertical. His departure, however, was opposite to what would be predicted if inflow influenced the perception of direction (inflow predicts that the fixation target would shift in the direction of the load).

We made some additional subjective observations that support this interpretation of our measurements. We pulled on the threads attached to the contact lens worn on the occluded right eye while S fixated the red target with his left eye. The red point appeared stationary no matter what was done to his right eye, which rotated freely. The S could report when and the direction in which we pulled his right eye, but neither slow nor rapid displacements caused shifts in the perceived direction or

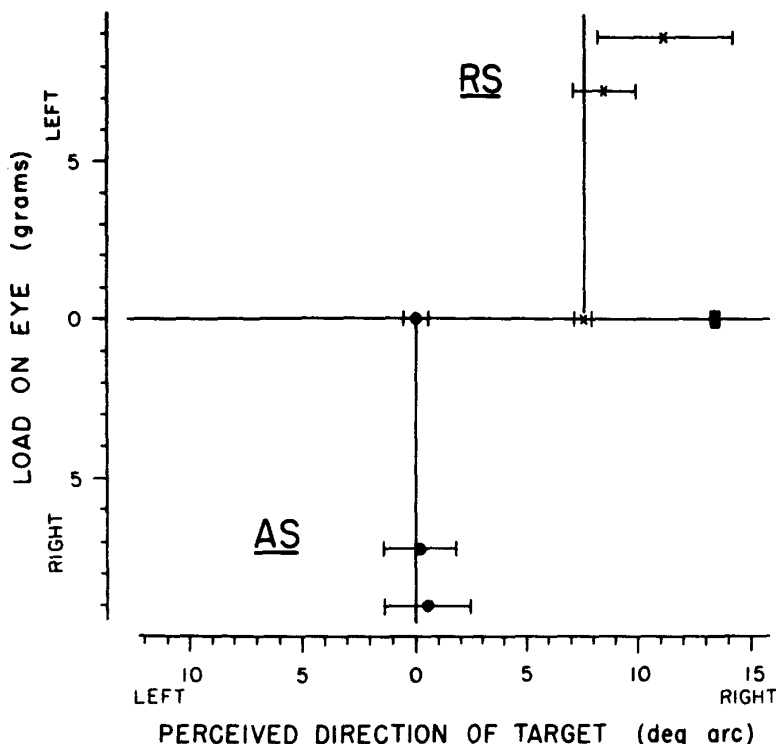


Fig. 3. Mean perceived direction of a fixation target for various loads applied to the left of S.R.S.'s right eye and to the right of S.A.S.'s right eye. The fixation target (seen by the left eye) was presented straight ahead for A.S. and right 13.5 deg of arc for R.S. (its objective position is shown by the rectangle). A.S. is shown by the circles and R.S. by crosses. Vertical lines show the perceived shift in target direction predicted from outflow theory. Each data point is the mean of 20 measures for A.S. and 12 for R.S. Error bars show one standard deviation on each side of the means.

movements of the red target fixated by his left eye. However, when we let the right eye see the red fixation target (left eye occluded) and then pulled on the right eye, the target danced all over. The E could easily produce what S said resembled slow autokinetic movements by pulling the eye gently from side to side. Heavy sustained pulls caused large shifts in the apparent direction of the red fixation target. It frequently appeared shifted beyond the largest possible rotation of the eye. On several occasions, S reported that he was looking completely to the side or even back of his head. This bizarre experience requires sustained loads we estimate to exceed 50 g. Large eye movements (>1 deg of arc) were not observed on the eye-position monitor during these manipulations, except when S was caught off guard by a sudden vigorous jerk.

In conclusion, our measurements show that the perception of direction depends primarily on the outflow to the extraocular muscles. The signal that flows into the oculomotor system from stretch receptors in these muscles has little or no influence on where a target appears in space—at least when the inflow message from one eye is in

conflict with the outflow sent to both eyes. These findings are not surprising, because Helmholtz came to the same conclusion a century ago from a number of ingenious subjective observations. We were, however, able to confirm and quantify, somewhat, the relationship between the innervation pattern and perceived direction and were also able to manipulate both inflow and outflow signals independently.

An important problem remains. Skavenski (1971) showed that the oculomotor system can process inflow information: these same Ss corrected passive displacements of their eyes introduced in total darkness and could report when and the direction in which the eye was pulled. Now that we know that the inflow signal does not influence their perception of direction, we would like to know what, if anything, inflow contributes to their control of eye position when they fixate or track a visible target.

REFERENCES

- ALPERN, M. Types of movement. In H. Davson (Ed.), *The eye*. New York: Academic Press, 1962. Pp. 91-93.
BRINDLEY, G. S., & MERTON, P. A. The absence of position sense in the human eye. *Journal of Physiology*, 1960, 153, 127-130.

- HELMHOLTZ, H. von. *Treatise on physiological optics*. (Trans. J. P. C. Southall) Vol. 3. New York: Dover, 1962. Pp. 242-246.
IRVINE, S. R., & LUDVIGH, E. J. Is ocular proprioceptive sense concerned in vision? *Archives of Ophthalmology*, 1936, 15, 1037-1049.
KELLER, E. L., & ROBINSON, D. A. Absence of a stretch reflex in extraocular muscles of the monkey. *Journal of Neurophysiology*, 1971, 34, 908-919.
KORNMEYER, A. E. Eine experimentelle Anästhesie der äusseren Augenmuskeln am Menschen und ihre Auswirkungen. *Journal of Psychology & Neurology*, Leipzig, 1931, 41, 354-366.
MATIN, L., MATIN, E., & PEARCE, D. Visual perception of direction when voluntary saccades occur. I. Relation of visual direction of a fixation target extinguished before a saccade to a flash presented during the saccade. *Perception & Psychophysics*, 1969, 5, 65-80.
PUCKETT, J. deW., & STEINMAN, R. M. Tracking eye movements with and without saccadic correction. *Vision Research*, 1969, 9, 695-703.
ROBINSON, D. A. The mechanics of human saccadic eye movement. *Journal of Physiology*, 1964, 174, 245-264.
ROBINSON, D. A. The oculomotor control system: A review. *Proceedings of the I.E.E.E.*, 1968, 56, 1032-1049.
SHERRINGTON, C. S. Observations on the sensual role of the proprioceptive nerve-supply of the extrinsic ocular muscles. *Brain*, 1918, 41, 332-343.
SKAVENSKI, A. A. Extraretinal correction and memory for target position. *Vision Research*, 1971, 11, 743-746.
SKAVENSKI, A. A. Inflow as a source of extraretinal eye position information. *Vision Research*, 1972, 12, 221-229.
SKAVENSKI, A. A., & STEINMAN, R. M. Control of eye position in the dark. *Vision Research*, 1970, 10, 193-203.
STEINMAN, R. M., CUNITZ, R. J., TIMBERLAKE, G. T., & HERMAN, M. Voluntary control of microsaccades during maintained monocular fixation. *Science*, 1967, 155, 1577-1579.

NOTES

1. The color of the target did not have marked effects on the location of the subjective straight ahead. The placement of the red fixation target in this position was based on preliminary measurements of the subjective straight ahead made with the movable white target seen in total darkness. During the experiment, when the unloaded eye was used to fixate the red target, the white target was always judged to be straight ahead when it was near the red target. We believe that the red fixation target was really "straight ahead" and that S was not simply aligning the white target to the red target's position, because the variability in positioning the white target was much greater than that typically observed in vernier tasks.
2. The evidence for good yoking is based on demonstrations that Hering's law holds even under dichoptic viewing conditions with unencumbered eyes (Alpern, 1962). Also, it is unlikely that a passive displacement of an eye would change the outflow to that eye, because it is currently believed that a local stretch reflex (of the kind found in skeletal muscles) is not found in extraocular muscle (Keller & Robinson, 1971; Robinson, 1968).
3. There have been a number of fine experiments which have dealt with the quality and nature of the extraretinal signal involved in the visual perception of direction. Many of these experiments have been discussed in detail elsewhere (Skavenski, 1971b) and will not be reviewed again here.

(Accepted for publication September 22, 1971.)