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INFLOW AS A SOURCE OF EXTRARETINAL EYE POSITION INFORMATION

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INTRODUCTION

SKAVENSKI and STEINMAN (1970) and SKAVENSKI (1971) have shown that there is an extraretinal signal of considerable fidelity that can be used to control eye position in total darkness.[2] There are at least two possible sources of this extraretinal eye position information. HELMHOLTZ (1866) proposed that our knowledge of eye position comes from the effort of will put forth in moving the eye. SHERRINGTON (1918), on the other hand, maintained that eye position information flows into the central nervous system from stretch receptors located in the extraocular muscles. Currently, HELMHOLTZ's (1866) "outflow" theory is widely accepted. Support comes from his observations on the effect of oculomotor activity on the perception of motion and direction. Namely, when the eye is passively displaced, the target, rather than the eye, is perceived as moving; and when the eye is restrained during attempted eye movement, the target is perceived as displaced in the direction of the attempted, but not executed, movement.

Although there is considerable evidence showing that there are stretch receptors in human extraocular muscles (BUZZARD, 1908; WHITTERIDGE, 1960) and that these receptors give rise to inflow signals in other animals (WHITTERIDGE, 1960; FUCHS and KORNHUBER, 1969), there is no evidence showing that such signals give rise to a sense of eye position. In fact, BRINDLEY and MERTON (1960) and IRVINE and LUDVIGH (1936), have shown that stimulation of stretch receptors in human extraocular muscles did not cause conscious sensations of changes in eye position.

However, the BRINDLEY and MERTON (1960) and IRVINE and LUDVIGH (1936) experiments do not conclusively demonstrate that the eye is without a conscious position sense because the psychophysical method of subjective reports used in these experiments is considered to be insensitive (BLACKWELL, 1952) and may not be adequate to detect a sense of eye position. Also the sensation of eye position may be subtle and could easily go unnoticed if S is distracted or under some degree of discomfort or duress. In one experiment, IRVINE and LUDVIGH (1936) pressed on the eye with a finger to produce passive displacements. This procedure produces marked sensations of pressure on the eyelid and eye which could mask subtle sensations of eye position caused by displacements of the globe. Also

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[2] An "extraretinal" signal is an eye position signal that does not arise from the relative location of a target image on the retina. MATIN, MATIN, POLA and PEARCE (1968) introduced this term so as not to prejudge whether the position information is proprioceptive or arises from the motor commands sent to the extraocular muscles.

IRVINE and LUDVIGH (1936) and BRINDLEY and MERTON (1960) passively displaced their *S*'s eyes by either grasping the conjunctiva with forceps or grasping the insertions of extraocular muscles with a forceps thrust through the conjunctiva. These procedures place *S* under duress and may cause him to overlook any proprioceptive information he may have about the position of his eye.

The experiments reported in the present paper show that *S*s can detect passive displacements of their eyes when a more sensitive psychophysical method, a forced choice technique (BLACKWELL, 1952), is used and when passive displacements of the eye are produced under more relaxing and less distracting circumstances. It will subsequently be shown that *S*s can use inflow information to control eye position in the dark.

EXPERIMENTS

1. *Subjects are aware of inflow information about eye position*

We can directly determine whether inflow provides a sense of eye position by silently applying forces to *S*'s eye (which would displace the passive eye) in total darkness and asking him to report when the load was applied, and also, the direction his eye was pulled. If only outflow information about eye position is available, *S* would not be able to respond correctly. This experiment was done as follows:

Two subjects (*RS* and *AS*) participated in the experiment. Both had considerable prior experience in eye movement experiments in which they were required to use both visual and extraretinal signals to control eye position, and both were accustomed to wearing tight-fitting, scleral contact-lenses.

External forces on the eye were produced by loads applied to a molded, tightly fitted, scleral contact-lens worn on the right eye. These lenses were held firmly in place by suction (7–12 mm Hg) and the eyes could be rotated large amounts without lens slippage. A 3-cm stalk was attached to the contact-lens and tangential forces were applied to this stalk by 2 calibrated containers (located to the left and right of the eye) which were attached to a ring that slipped over the stalk by means of threads that passed over pulleys.[3] These calibrated containers were connected to a hydraulic system with which known amounts of water could be gradually and silently added to either container. Thus, if water was added to the container on *S*'s left, its downward force was transmitted to the eye by the thread, causing a leftward displacement. The arrangement of the loading apparatus is shown in Fig. 1.

In this experiment, *S* was given a pump with which he could add water to either the left-pulling, right-pulling or a catch trial chamber (which was not connected to the eye). A set of valves permitted random connection of *S*'s pump to any one of the 3 chambers. Both of *RS*'s eyes were anesthetized by instilling 3 drops of 0·5 per cent Tetracaine Hydrochloride into each eye at 2-min intervals. Sixteen min after the first drop, the contact-lens was inserted and the experiment begun. *AS* participated without anesthesia.

A point target was presented 3 deg arc to the left of *RS*'s primary position and in the primary position for subject *AS*.

Trials began with 10 sec of fixation of the visible target with the right eye. The left eye was closed and covered. As soon as the target was switched off *S* sat in total darkness and began pumping water into one of the 3 chambers selected at random and unknown to *S*. *S* continued pumping water until he was satisfied that he had added water to a chamber that pulled his eye or to the catch trial chamber. He then reported either that his eye was loaded or that a catch trial had been run. When he said that his eye was loaded, he reported the direction his eye had been pulled. *S* was then given feedback and the quantity of water added on load trials was noted. Forty-four measurements were made by *RS* and 45 by *AS*. The last 9 were obtained with a disc of opaque tape occluding the corneal portion of the contact-lens to guarantee that these measurements had been made in total darkness. The experiment was replicated with a third *S* whose eye was not loaded. This *S*'s sole task was to try to guess which chamber was being filled with water when he pumped, using whatever cues he might find available in the experimental situation. His performance did not differ from chance.

Both *S*'s could detect the presence of a load and report the direction of the pull on his eye. Their performance is summarized in Table 1. *RS* never confused load with catch trials. His errors were always confusions of direction. *AS* called 1 left load trial a catch trial and also called 2 catch trials as load trials. His other errors were like those of *RS*, confusions in the direction of the load. A chi-square test of frequencies of each type of response showed that both *S*s correctly identified each type of load on a significant proportion of the trials ($p < 0.001$). Both *S*'s must, then, have been aware of inflow information about eye position.

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[3] A closed system was used to prevent spillage and evaporation. The "calibrated containers" were actually plastic syringes with rubber pistons in place. Plastic plungers, normally used to move the rubber pistons, were removed in order to reduce the weight of the empty syringes.

TABLE 1. RELATIVE FREQUENCIES OF CORRECT RESPONSES FOR THREE TYPES OF TRIALS

Subject	Trial type: Load right	Load left	No load	Load (g) (S.D.)
RS	11/15	12/16	13/13	10·0 (6·9)
AS	14/16	11/14	13/15	8·7 (5·5)
RS	14/17	13/19	17/19	14·0 (4·7)

Loads are also shown (standard deviations are given in parentheses). The last row summarizes *RS*'s performance when his eyelids had been injected with anesthetic and retracted so they could not touch the contact-lens (described in text).

The measurements were repeated for *RS* under conditions where mechanoreceptors in anterior portions of his orbit could not give any indication of eye position or of forces applied to his eye. Once again 0·5% Tetracaine Hydrochloride was placed in both eyes, as described previously, after *RS*'s eyelids had been injected with 2% Lidocaine Hydrochloride (epinephrine 1:100,000). Since such local anesthetics may not remove all sense of touch, a further precaution was taken that both eyelids were retracted and held away from all possible contact with the scleral contact-lens. The psychophysical procedure was the same as outlined above. The results are summarized in the last row of Table 1. *RS* confused 2 load trials with catch trials. All other errors were confusions in the direction the load was applied. A χ-square test of the frequencies of each type of response, once again, showed that *RS* correctly identified each type of load on a significant proportion of the trials ($p < 0{\cdot}001$). The inflow signal must then, arise from receptors further back in the eye.

Loads (g) applied tangential to the eye are also shown in Table 1. Based on the spring (tension/length) constant, measured for these *S*s (by a procedure described later in text) these loads correspond to rotations of the passive eye of from 10 to 14 deg arc for *RS* and about 7 deg arc for *AS*. Actually these loads were large enough to suggest that general pressure cues (from retrobulbar mechanoreceptors or from the slight warping of the eyeball at the edges of the contact-lens that occurs when loads are applied) were providing *S* with enough information to judge when, and in which direction, the eye was pulled. The next experiment indicates that this was not the case.

2. *Inflow can be used to control eye position in the dark*

We can determine whether inflow can be used for oculomotor control by passively displacing the eye while a subject attempts to maintain eye position in the dark.[5] If only outflow information about eye position is available, and if the inflow that is available is not position information, then the subject would not be able to correct the error introduced by the passive displacement. This experiment was done as follows:

Horizontal eye positions were recorded by means of a diffuse reflection technique. In this method a photoresistor measures the amount of diffuse infrared light (9000 Å ± 40) reflected from the limbus (where the white sclera joins the dark iris). With suitable calibration and linearizing procedures, horizontal positions of the eye could be measured to within 0·5 deg arc over a 16-deg arc range. The arrangement of the recording apparatus may be seen in Fig. 1.

The apparatus and experimental conditions were exactly the same as in the previous experiment except that *E* controlled the pump which added water to the right-pulling, left-pulling or catch trial chamber.

The target was presented 3 deg arc to the left of *RS*'s primary position and in the primary position for subject *AS*. *RS*'s conjunctiva were anesthetized by instilling 3 drops of 0·5% Tetracaine Hydrochloride in each eye at 5-min intervals. Five min after the third drop, the contact-lens was inserted and the experiment began. *AS* participated without anesthesia.

At the beginning of each experimental session, the amount of water needed to produce known passive eye rotations (of about 5 deg arc) was determined by ROBINSON's (1964) technique for measuring spring constants (tension/length) of the human eye.[6] In this procedure, *S* fixated a target visible only with his unencumbered left eye while loads were applied to his occluded right eye. Since the 2 eyes are yoked very well,

[5] See A. A. SKAVENSKI and R. M. STEINMAN (1970) for the characteristics of extraretinal control for periods up to 2 min and A. A. SKAVENSKI (1971) for extraretinal control during 7·5 min in darkness and following a 15-min period of normal visual activity. Briefly, eye position was generally less than about 2 deg arc from the target during 2-min periods and less than 4 deg arc from the target during 7·5-min periods of total darkness.

[6] Spring constants measured for the present *S*s were similar to those reported by ROBINSON (1964): 1·0 g/deg arc rotation for *RS*, 1·3 g/deg arc for *AS*, and 1·25 g/deg arc for Robinson's *S*s.

fixation of the target with the left eye maintained a constant innervation pattern to the extraocular muscles of the right as it was passively displaced by the addition of water to one of the chambers. Spring constants were determined and used to select volumes of water that would passively displace the right eye by desired amounts.

After the spring constants were measured, *S*'s left eye was covered and the occluder was removed from his right eye. Trials began with 10 sec of fixation of the visible target. The target was then switched off and the load was gradually applied. Loading was completed in about 5 sec and *S* spent the next 20 sec attempting to keep his eye in the position the target had previously been seen, at which time, the load was gradually removed. The eye was always completely unloaded before the end of the 34-sec dark period when the target reappeared. On about 1/3 of the trials no load was applied and the order of these, as well as the left and right load trials was randomized. Fourteen trials were run for *RS* (5 rights, 5 lefts and 4 no load) and 17 trials (6 of each load and 5 no load) were run for *AS*.

For each trial 2 horizontal eye positions were randomly sampled from each second of the 8-sec period just prior to target disappearance and during the 18-sec period when the load was fully applied just prior to the time *E* began removing the load). *Error* (the distance between mean eye position when the eye was not loaded and mean eye position when the eye was loaded) was used to evaluate *S*'s ability to use inflow information to keep his eye in the position defined when the target was visible. Mean *errors* are summarized in Table 2 along with the passive displacements produced by the same loads using ROBINSON's (1964) technique (see above).

TABLE 2. MEAN ERROR WHEN SUBJECTS *RS*'S AND *AS*'S RIGHT EYES WERE PASSIVELY DISPLACED (Passive) AND WHEN THEY ATTEMPTED TO MAINTAIN EYE POSITION (Corrective) UNDER Right AND Left LOADS

Direction ot load	Error (deg arc) (S.D.) Passive trials	Error (deg arc) (S.D.) Corrective trials
	Subject *RS*	
Right	2·5 (0·1)	0·7 (1·1)
Left	−7·1 (1·5)	−0·8 (0·8)
	Subject *AS*	
Right	6·1 (0·4)	−2·0 (1·4)
Left	−5·1 (0·7)	−3·3 (1·8)

Standard deviations of the observations are given in parentheses. Negative errors signify that the eye was to the left of the target position.

Both *S*s were able to keep their eyes near the target position when loads were applied during the dark period. The *errors* that occurred when these *S*s corrected for loads are of about the same magnitude as the *errors* they made when they used extraretinal signals to control eye position in the dark with no external forces applied to their eyes (see Footnote Fig. 1). By the sign test, correction for loads was significant for both *RS* ($p < 0{\cdot}01$) and *AS* ($p < 0{\cdot}02$).

For *RS* the right load was selected so as to produce passive displacements of only 2·5 deg arc.[7] *RS*'s left load was selected to produce much larger displacements (7 deg arc). Small, as well as large, inflow signals could be processed equally well by this subject. *AS*'s maintenance of eye position under the loaded condition was somewhat poorer than that of *RS* but he also showed correction.[8] Representative recordings of passive displacement and active correction trials are reproduced in Fig. 2.

The records show that neither *S* allowed large errors to build-up before he began corrective action. Both compensated appropriately for small changes in the applied force or orientation of their eyes.

In summary, both subjects could keep their eyes near target position in the dark when a force, which

[7] This displacement was chosen to be somewhat less than this *S*s error during 7·5-min periods of extraretinal control in prior experiments (SKAVENSKI, 1971).

[8] *AS*'s mean error was about 2–3 deg arc to the *left* of target position irrespective of the direction of the load. A similar left-bias was observed when *AS* used extraretinal signals to control eye position in prior experiments. In prior experiments *AS*'s eye moved to the left of target position soon after the target was removed from view on about 90% of the trials. In the present experiment, *AS*'s eye also rotated to the left of target position on 11 of the 12 trials during which he attempted to correct for load. If allowance is made for *AS*'s left bias, his correction for loads was about as good as his unencumbered control of eye position in the dark.

FIG. 1. Subject *RS* in position in the apparatus used to record horizontal eye movements while loading his right eye. *RS* is biting on an acrylic bite board which holds his head rigidly in place. Horizontal rotations of his right eye were recorded (for purposes described later in text) by means of an i.r. light transmitting and a collecting fiber optic mounted on the microscope stage just to his right. Loads were applied by adding water to the plastic chambers shown below the pulleys on the left and right. Loads were transmitted to the eye by means of the dacron threads that pass over the pulleys and connect to the 3 cm stalk attached to the scleral contact-lens. The contact-lens was held firmly to the eye by suction applied through the thin polyethylene tubing that can be seen as it passes up over the bridge of the nose and, again, as it passes in front of the left eye patch on its way to the suction apparatus (not shown).[4] With this apparatus loads of various magnitudes could be applied to the right eye gradually and completely silently.

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[4] Note, the section tubing was arranged so that it did not, at any time during these experiments, touch the nose or face at any place except where it was taped to the forehead near the hairline. This contact with the skin could not have provided eye position information because the lateral displacement of the end of tubing at its junction with the contact-lens was too small and the tubing too flexible to produce any tactile cues on the forehead.

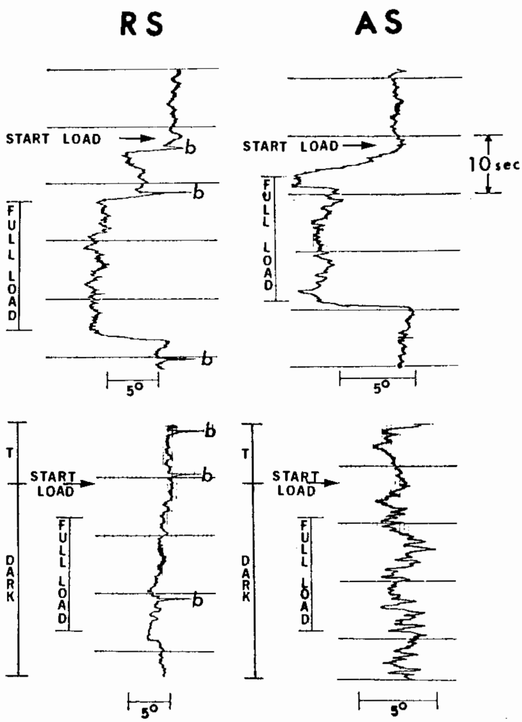

FIG. 2. Representative recordings of *RS*'s and *AS*'s horizontal eye position control when loads were applied to their right eyes. In the upper records *S*s fixated the visible target with their left eyes. Right eyes were occluded. Application of the load began at the time indicated by the arrow head and the vertical bar on the left indicates the period of time the *full load* was applied. The final seconds of each record show eye position returning to baseline as the load was removed. The two lower records show *RS*'s and *AS*'s ability to correct eye position when loads, equal to those applied in the upper records, were applied during the dark period. For these records *S*s right eyes were uncovered and their left eyes were closed and covered. Records begin with 10 sec of fixation of the visible target (*T*). The target was switched-off at the time indicated by the arrow and the remainder of the record shows eye position control in the dark (*DARK*). Application of the load began just after the time indicated by the arrow and the vertical bar shows the period the *full load* was applied. The load was removed during the final seconds of each record. Pulse-like changes in the trace, labelled *b*, are blinks. Horizontal bars beneath each record show 5 deg arc rotations on the horizontal meridian.

would have displaced the passive eye, was applied. These corrective movements could not have been guided by ouflow information: neither the subject's memory of the innervation pattern used to fixate the visible target nor his memory of eye movements made after target disappearance would be sufficient to correct for the loads applied in the dark. Because outflow could not provide a reliable indication of eye position in this experiment, the subject's good control of eye position indicates in inflow signal must have been available. Furthermore, the inflow information must be of a positional nature because it is unlikely that a general, deep pressure sense could have provided the quality of position information required to explain the good control of eye position observed in this experiment.

DISCUSSION

The present experiments show that subjects are aware of inflow information about eye position. Furthermore, these inflow signals are accessible to the oculomotor system for the control of eye position in the dark. Note, it is only claimed that inflow information can contribute to our extraretinal knowledge of eye position; not that inflow is the sole source of extraretinal position information. The techniques used in the present experiments do not permit an assessment of the relative contributions of inflow and outflow to extraretinal eye position information nor do they rule out outflow.

Finding that inflow (or proprioception) can contribute to our knowledge of eye position was previously reported by LUDVIGH (1952). He found that, during a short dark interval, a single target must be moved "substantially in excess of 6 degrees" before "the observer could state with high reliability" whether it had been displaced to the left or to the right of its initial position (p. 439). LUDVIGH (1952) claimed that "the proprioceptive sense cannot reliably furnish information adequate for determination of the position of the eye to an accuracy of better than 10 degrees". However, this claim is too broad because the task lumps together both inflow and outflow eye position information. Also, other investigators (e.g. FIORENTINI and ERCOLES, 1966; MATIN, PEARCE, MATIN and KIBLER, 1966; MERTON, 1961; MILLER and HALL, 1962) using tasks very similar to Ludvigh's, have all reported that our visual spatial sense, in the absence of visual cues to direction, is much more accurate (by about one order of magnitude) than LUDVIGH (1952) found. From the experiments just cited, it is clear that our extraretinal knowledge of eye position is reasonably good. Unfortunately, it is difficult to know, from these same experiments, what contribution inflow makes to extraretinal eye position information because, as in LUDVIGH's (1952) experiments, normal inflow and outflow were both available to *S*, i.e. *E* did not assess the effect of disrupting either inflow or outflow on the perception of direction.

Of those experiments (e.g. BRINDLEY and MERTON, 1960; HELMHOLTZ, 1866; IRVINE and LUDVIGH, 1936) that did directly assess the contribution of inflow to extraretinal eye position information, all agree that inflow does not give rise to a conscious awareness of eye position even when passive displacements of the eye were as large as 40 deg arc. The present finding, that *S*s were consciously aware of the direction of passive displacements of the eye, does not agree with these previous reports. These conflicting results are probably due to differences in the procedures used in the various experiments. Forced choice psychophysical procedures of the kind used in the present experiment are more sensitive than subjective reports (BLACKWELL, 1952). Also, the sensation of eye position (like the sensation of limb position) is subtle. Both could easily go unnoticed if *S* is distracted or is subjected to surgical insults (e.g. pulling on the insertion of an extraocular muscle with a forceps thrust through the conjunctiva). Similarly, a subject *might* find it difficult to attend the position of a finger when the upper arm, in the region of the elbow, was very firmly grasped and held in place. The sensation of pressure on the arm in this case is uncomfortable and distracting and is analogous to pressure on the eye in HELMHOTLZ's (1866) and IRVINE and LUDVIGH's (1936) experiments.

Another explanation for the conflict in results may lie in the prior histories of the *S*s in the present and previous experiments. Although the past histories of BRINDLEY's *et al.* (1960), HELMHOLTZ's (1866) and IRVINE's *et al.* (1936), *S*s were not documented, it seems safe to assume that they had much less experience maintaining eye position in total darkness than *RS* and *AS* in the present experiments (see SKAVENSKI and STEINMAN, 1970; SKAVENSKI, 1971). It is possible that extensive oculomotor control in the dark enables *S*s to feel more confident about using, and also to better attend to, more subtle information about eye position. Others (MILLER and HALL, 1962 for example) have reported that subjects, when exposed to a structureless visual field (a Ganzfeld or total darkness), hurriedly search for fixation targets in order to orient themselves. It is possible that BRINDLEY's *et al.* (1960), HELMHOLTZ's (1866), and IRVINE's *et al.* (1936) *S*s experienced a similar uncertainty about eye position in a visual field without fixation points because they have not had the opportunity to become accustomed to the reduced information about eye position. In other words, requiring *S*s to make a response as to the position of their eyes in the absence of visual cues is a novel situation and *S*s may be unable to do so because they have never tried to use their eye position sense.

While the reason for the discrepancy with prior experiments remains obscure, the results of the present experiments are clear: *S*s *are* consciously aware of inflow eye position information and inflow information *can* be used by the oculomotor system to control eye position in the dark.

The loads required for detection in the psychophysical procedure (Section 1) were larger than the loads applied when *RS* and *AS* corrected eye position in the previous experiment (Section 2). Since these *S*s could correct eye position for smaller loads than they required for the psychophysical report, it is possible to suggest that the oculomotor response is more sensitive and perhaps unconscious. This suggestion, although provocative, is only tentative because the absolute threshold was not measured. *S*s adopted a high criterion in the psychophysical procedure evidenced by the fact that they very seldom said a load was applied to their eyes when it was not. The absolute threshold would probably be much lower than the loads shown in Table 1 if measured by practiced observers who adopt a lower criterion.

In conclusion, the present experiments show that there is an extraretinal inflow signal that does not arise from the conjunctiva or eyelids. It must arise, then, from receptors further back in the eye. Retrobulbar mechanoreceptors and stretch receptors in the extraocular muscles are possible sources. Retrobulbar mechanoreceptors are suggested because it is currently believed that stretch receptors, elsewhere in the body, do not provide a conscious sense of body position (GELFAN and CARTER, 1967; PROVINS, 1958; ROSE and MOUNTCASTLE, 1960). However, these experiments were relatively crude and more sophisticated psychophysical methods may yield different results concerning the role of stretch receptors in the conscious body position sense. Also, the possibility that retrobulbar mechanoreceptors are responsible for our sense of eye position should be viewed with caution because such receptors have not been demonstrated anatomically.

Further implications of the present findings for an understanding of oculomotor control and visual perception of direction and motion are not clear. The present experiments were designed only to detect the presence of an awareness of extraretinal inflow signals and to show that they can be used for oculomotor control; not to determine how these inflow signals are normally used. Further speculation about the storm of controversial questions concerning when and for what purpose these signals are used must await more extensive investigations which directly assess their functional significance.

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REFERENCES

BLACKWELL, H. R. (1952). Studies of psychophysical methods for measuring visual thresholds. *J. opt. Soc. Am.* **42,** 606–616.

BRINDLEY, G. S. and MERTON, P. A. (1960). The absence of position sense in the human eye. *J. Physiol., Lond.* **153,** 127–130.

BUZZARD, E. F. (1908). A note on the occurrence of muscle-spindles in ocular muscles. *Proc. R. Soc. Med.* **1,** *Neurological Section,* 83–87.

FIORENTINI, A. and ERCOLES, A. M. (1966). Visual direction of a point source in the dark. *Atti Fond. Giorgio Ronchi* **23,** 405–428.

FUCHS, A. F. and KORNHUBER, H. H. (1969). Extraocular muscle afferents to the cerebellum of the cat. *J. Physiol., Lond.* **200,** 713–722.

GELFAN, S. and CARTER, S. (1967). Muscle sense in man. *Expl Neurol.* **18,** 469–473.

HELMHOLTZ, H. VON (1866). *Handuch Der Physiologischen Optik.* Voss, Leipzig. English translation, from *A Treatise on Physiological Optics* (edited by J. P. C. SOUTHALL) Edn. 3 (1925), Vol. 3 (1963). Dover, New York.

IRVINE, S. R. and LUDVIGH, E. J. (1936). Is ocular proprioceptive sense concerned in vision? *Archs Ophthal.* **15,** 1037–1049.

LUDVIGH, E. J. (1952). Possible role of proprioception in the extraocular muscles. *Archs Ophthal.* **48,** 436–441.

MATIN, L., MATIN, E., POLA, J. R. and PEARCE, D. (1968). Visual perception of direction before, during and after voluntary saccades. Paper read at Psychonomic Society Meeting at St. Louis, Missouri, Oct., 1968.

MATIN, L., PEARCE, D., MATIN, E. and KIBLER, G. (1966). Visual perception of direction in the dark: roles of local sign, eye movements, and ocular proprioception. *Vision Res.* **6,** 453–469.

MERTON, P. A. (1961). The accuracy of directing the eyes and the hand in the dark. *J. Physiol., Lond.* **156,** 555–577.

MILLER, J. and HALL, R. (1962). The problem of motion perception and orientation in the Ganzfeld. *Visual Problems of the Armed Forces* (edited by MILTON A. WHITCOMB). National Academy of Sciences–National Research Council, Washington, D.C.

PROVINS, K. A. (1958). The effect of peripheral nerve block on the appreciation and execution of finger movements. *J. Physiol., Lond.* **143,** 55–67.

ROBINSON, D. A. (1964). The mechanics of human saccadic eye movement. *J. Physiol., Lond.* **174,** 245–264.

ROSE, J. R. and MOUNTCASTLE, V. B. (1960). Touch and kinesthesia. In *Handbook of Physiology: A Critical, Comprehensive Presentation of Physiological Knowledge,* Section 1, *Neurophysiology* (edited by J. FIELD, H. W. MAGOUN and V. E. HALL) Vol. 1, chap. 17, pp. 409–415. American Physiological Society, Washington, D.C.

SHERRINGTON, C. S. (1918). Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain* **41,** 332–343.

SKAVENSKI, A. A. (1971). Extraretinal correction and memory for target position. *Vision Res.* **11,** 743–746.

SKAVENSKI, A. A. and STEINMAN, R. M. (1970). Control of eye position in the dark. *Vision Res.* **10,** 193–203.

WHITTERIDGE, D. (1960). Central control of eye movements. In *Handbook of Physiology: A Critical Comprehensive Presentation of Physiological Knowledge,* Section 1, *Neurophysiology* (edited by J. FIELD, H. W. MAGOUN and V. E. HALL), Vol. II. Chap. 42, pp. 1089–1109. American Physiological Society, Washington, D.C.

Abstract—Two subjects could reliably report when, and in which direction, loads were applied to their eyes in total darkness indicating that they were aware of inflow (afferent) eye position information. Awareness of the inflow signal was not disrupted when the eyelids and conjunctiva were anesthetized and the eyelids were retracted from all possible contact with the scleral contact-lens. Furthermore, the subjects maintained eye position, when loads were applied to the eye in total darkness, showing that this inflow information can be used for extraretinal oculomotor control.

Résumé—On a constaté sur deux sujets une certitude de savoir quand et dans quelle direction des charges étaient appliquées à leurs yeux dans l'obscurité totale, ce qui indique qu'ils perçoivent des signaux afférents qui les informent de la position des yeux. Cette perception subsiste après anesthésie des paupières et de la conjonctive, et suppression de tout contact possible entre les paupières et la lentille sclérale. En outre les sujets maintiennent la position du regard quand on applique des chatges à l'oeil dans l'obscurité totale, montrant que cette information afférente peut servie à contrôler le système oculomoteur par des moyens extrarétiniens.

Zusammenfassung—Zwei Versuchspersonen konnten verläßlich berichten, wann und in welcher Richtung in völliger Dunkelheit Gewichte an ihre Augen angelegt wurden. Das zeigt, daß sie sich der ankommenden (afferenten) Information über die Augenstellung bewußt waren. Dieses Bewußtsein wurde nicht unterbrochen, wenn die Augenlider und die Konjunktiva anästhesiert wurden und jeder mögliche Kontakt zwischen der skleralen Haftschale und den Augenlidern verhindert wurde. Darüber hinaus konnten die Versuchspersonen die Augenstellung beibehalten, wenn Belastungen an das Auge in völliger Dunkelheit angelegt wurden. Das zeigt, daß die afferente Information für extraretinale oculomotorische Kontrolle verwendet werden kann.

Резюме—Два испытуемых могли увереннос ообщать о том, когда и в каком направлении к их глазам в полнойтемноте прикладывался вес, что указывало на то, что они отдавали себе полный отчет о поступающей (афферентной) информации о положении глаз. Зта информация не нарушалась, если веки и конъюнктива были анестезированы и веки были оттянуты во избежание всякого соприкосновения со склеральной контактной линзой. Более того, испытуемые сохраняли положение глаз, когда вес прилагался в темноте. Зто указывает на то, что данная информация может быть использована для зкстраретинального двигателвного контроля.