

MINIREVIEW

PROPRIOCEPTIVE KNOWLEDGE OF EYE POSITION

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Abstract—The peripheral and central apparatus for extraretinal (non-visual) sensing of eye position by proprioception (inflow) is documented. The functional significance of this inflowing signal is shown by its role in (1) providing oculomotor stability in fixation and conjugacy, (2) specification of visual direction, (3) development of some visual functions, and (4) depth and vergence responses. Inflow is seen as a slowly-operating calibrator of eye position, with outflow signals read out from the underlying inflow signal. Good "preparations" for studying inflow include humans having their extraocular muscles surgically manipulated in some way for treatment, or those with some deficit in the afferent pathways. A complete understanding of the oculomotor system, in normal and pathological conditions, demands the inclusion of inflow.

Proprioception Inflow Eye muscles Oculomotor control Eye movements Strabismus
Binocular vision

INTRODUCTION

How does the brain stay informed about which way the eyes are pointing? There are three possible sources of information, and they are not mutually exclusive: (1) vision; (2) efferent ("outflow") or corollary discharge signals sent to the eye muscles; (3) afferent ("inflow") signals from proprioceptors in the muscles and tendons of the eye. In the absence of vision it is clear that eye position information is available (Matin, 1986) and it is believed by most researchers that outflow provides the only useful extraretinal signal. Helmholtz is usually given primacy for this view but it can be traced further back (Grüsser, 1986).

There are grounds for excluding a proprioceptive source for eye position: (1) the nearly-spherical globe's center of rotation and center of gravity are virtually the same and therefore (unlike the skeletal motor system) gravity does not contribute to the force required to move the eye to any position in its orbit. Except in pathology, the muscles operate under an unchanging load (Howard, 1982). (2) Diligent searching has failed to find a stretch reflex in a

primate (Keller and Robinson, 1971). (3) There are numerous demonstrations indicating that outflow (corollary discharge) to the muscles is used to specify the position of the eye in the orbit (see e.g. Carpenter, 1977; Guthrie *et al.*, 1983). Is there evidence to suggest that inflow is important? I believe the answer is yes and this review will briefly cover the anatomy and physiology of eye muscle proprioception, *briefly* because there can be no question that the peripheral and central mechanisms are in place. Most of the effort will be spent grappling with the question of what function extraretinal inflow may have.

ANATOMY

Receptors

There are muscle spindles and Golgi tendon organs (GTOs) in the eye muscles of man (Cooper and Daniel, 1949; Cooper *et al.*, 1955; Hosokawa, 1961; Barker, 1974). In addition, there are numerous palisade endings located at the musculotendinous junction (Richmond *et al.*, 1984; Mukuno, 1987). For the spindle-free cat and those species of monkey that are spindle-free, the palisade ending appears to be a primary proprioceptor because of its relative abundance and the paucity of traditional GTOs

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(Alvarado-Mallart and Pincon-Raymond, 1979; Ruskell, 1978, 1979). Richmond *et al.* (1984) noted the absence of traditional GTOs in their samples of human muscle and Golgi himself overlooked the few endings that are known to exist in human tendon (Eggers, 1982). Spiral nerve endings on extrafusal fibres had also been considered to be sensory structures in man but Ruskell (1984) has shown they terminate in motor end plates.

Central connections

In monkeys, cats and ungulates the proprioceptors are innervated by ipsilateral neurons of the trigeminal nerve ganglion (see e.g. Manni and Bortolami, 1982; Porter and Spencer, 1982; Porter *et al.*, 1983; Ogasawara *et al.*, 1987). The peripheral processes travel up the motor nerves and cross to the ophthalmic division of the trigeminal nerve. A similar situation is assumed in man, and the anastomoses between motor and trigeminal nerves are believed to occur in the cavernous sinus (Doxanas and Anderson, 1984). Porter (1986) has shown that, in the monkey, these neurons project to the ipsilateral spinal trigeminal and cuneate nuclei. He further believes that the myotendinous cylinder (palisade ending) is the receptor responsible for most of the terminal labelling he observed in these sites. Connections after the dorsal horn have yet to be worked out in detail, but there is electrophysiological evidence for widely distributed signals.

PHYSIOLOGY

Stretching the eye muscles evokes responses in a number of brain areas. In the cat, for example, they have been recorded from the reticular formation (Fillenz, 1955), the superior colliculus (Rose and Abrahams, 1975; Donaldson and Long, 1980), the cerebellum (Fuchs and Kornhuber, 1969; Baker *et al.*, 1972; Schwarz and Tomlinson, 1977) and the visual cortex (Buisseret and Maffei, 1977). Recent reviews are available (e.g. Bach-y-Rita, 1975; Manni and Bortolami, 1982; Maffei and Fiorentini, 1984).

There is a fundamental problem in all studies using passive stretch to provoke proprioceptive responses: one cannot be sure the responses mimic those present when the muscle contracts naturally, i.e. with alpha-innervation. Voluntary movement is carried out with the co-contraction of alpha (extrafusal) and gamma (intrafusal) fibres (Granit, 1975) and this probably produces

a different afferent signal than the one produced artificially. Some inputs may even be missing: the palisade endings, for example, are embedded in the stiff collagen of the tendon while terminals invest the end of the extrafusal fibre. The collagen may insulate these receptors from the effects of passive stretch (Richmond *et al.*, 1984; Ruskell, 1978). Spielmann and Stauffer (1986) recently showed in cat soleus muscle that the most "physiologically relevant" stimulus for the Golgi tendon organ was from the muscle unit attached directly in series with the receptor. These considerations make the study of responses from eye muscle receptors very difficult to interpret and, in addition to the relative inaccessibility of the afferent pathways, may account for the relative paucity of physiological research on the topic (a recent symposium on the muscle spindle did not even mention extraocular muscle spindles—Boyd and Gladden, 1985).

There is another problem in understanding how receptors that are apparently signalling tension (tendon organs, palisade endings) can provide unambiguous information about the position of the eye in the orbit. Collins (1975) has shown that for two very different eye positions in humans the tension recorded (near the insertion) using in-series strain gauges can be identical. An intact oculomotor system may resolve this ambiguity by taking into account the tension responses from all six extraocular muscles at the same time.

FUNCTION

A most vexing problem in trying to understand the role of proprioception is to come up with some clear, unequivocal evidence for its function. Evidence for inflow playing a role in supplying position information about the eye in the orbit is coming from several different directions, outlined below. Another concern involves reconciling the obvious use of outflow with the seemingly redundant inflow signal.

Stability: conjugacy and fixation

Westheimer (1975, 1982) reminds us of Hering's observations that people who have been blind in one eye from birth still have apparently perfectly conjugate eye movements as adults. A good reason for not accepting that this conjugacy is hard-wired is that the developing system is then able to make adjustments during periods of growth. This plasticity in the person blind in

one eye requires a non-visual sensing of eye position, i.e. proprioception. Westheimer (1982) likens this to a homeostatic process for maintenance of conjugacy, without the use of diplopia. Meredith and Goldberg (1986) have shown just how complicated a task the central nervous system has in maintaining conjugacy: the medial and lateral rectus muscles have different contractile properties, requiring different amounts of innervation during shifts of fixation in horizontal eye movements.

In the absence of binocular vision this conjugacy may not be perfect, as careful monitoring of eye movements (using a coil technique) has shown, Viirre *et al.* (1987) patched one eye of monkeys for a 1-week period and observed the movements of the patched eye during that period. They found (usually) a 10% decrease in saccadic step magnitude with a post saccadic drift in the patched eye. In some monkeys these changes were asymmetric with orbital position and with the direction of eye movement. The authors noted that repetitive pairs of saccades did not lead to a progressive shift of the position (because of the accumulation of error) of the occluded eye in the orbit. The slow drift that prevented this must be attributable to some non-visual sensing and correction of the post-saccadic position of the eye.

The notion that proprioception can be supplying some sort of stability signal for fixation (and not just to maintain conjugacy) is shown in the results of Fiorentini and Maffei (1977). They cut the ophthalmic division of the trigeminal nerve in the cat, a proprioceptively deafferenting procedure, and found large oscillations of the eyes in the dark. Humans with congenital nystagmus also exhibit a form of fixation instability and Optican and Zee (1984) have suggested that an abnormality in afference may be responsible. Magnin *et al.* (1986) immobilized one eye in cats by severing the III, IV and VI cranial nerves. In the dark, they found oscillations of the non-paralyzed eye, attributing them to the presumed disruption of afference that would follow severing the motor nerves distal to the point of the afferents' convergence with the ophthalmic nerve.

Specification of visual direction

The first important study suggesting that inflow may play a role in specifying eye position in humans was that of Skavenski (1972). Using two highly trained observers, he was able to demonstrate the presence of a crude message

about passive displacement of the eye in the dark. These results were very difficult to obtain and show quite clearly how feeble the inflow signal is: these practised subjects, while sensing a displacement of the eye, had to guess its direction. Skavenski *et al.* (1972) were also able to show that when there was a conflict between inflow and outflow information, the visual system made use of the outflow signal to specify visual direction. Why this should be is discussed later.

Recently there has been interest in studying the human with oculomotor pathology or surgical manipulation of the eye muscles as a "preparation" for studying the role of proprioception. For example, Campos *et al.* (1986) tested spatial localization in patients with active herpes zoster ophthalmicus. In this condition the ophthalmic division of the trigeminal is infiltrated by a virus, effectively deafferenting the structures innervated by this nerve (patients, for example, experience corneal anesthesia during a flare up). Assuming that proprioceptive afference flows up the ophthalmic division (this is not known for certain in man), Campos *et al.* measured open-loop pointing responses (the patients pointed to targets without being able to see their hands) and found constant errors of localization only during the active phase of the infection. The errors declined with recovery. These are good patients to study because there is usually no motor involvement with this form of herpes, i.e. eye movements were normal even during the active phase of the infection. Deafferented cats also show localization errors (Fiorentini *et al.*, 1982).

Using strabismus patients undergoing surgery to re-align the eye, Steinbach and Smith (1981) found evidence for proprioceptively-derived information about eye position in patients being operated on for the first time. Open-loop pointing responses were surprisingly accurate in patients whose eyes were surgically rotated and who did not have any visual experience in those eyes until the moment of testing. This could only occur if they had information available about the eye's new position, and, in the absence of vision, this could only have come from a proprioceptive source. Bock and Kommerell (1986) failed to replicate this finding but crucial differences in anesthetic techniques may be responsible. Kommerell (personal communications) used a retrobulbar injection of local anesthetic to perform the surgery whereas Smith's patients were all under general anesthe-

sia. The infiltration of topical anesthetic in the retrobulbar space probably knocked out proprioceptive as well as pain afferents, and this could be the reason that Bock and Kommerell found no evidence for proprioception in their patients.

Steinbach and Smith (1981) suggested that the musculotendinous region contained proprioceptors important for specifying eye position. This suggestion was based on the findings that patients who had had the same muscles operated on in repeated procedures did not appear to have inflow information about eye position. The anatomical examination of the site of surgery led to the finding of palisade endings (Richmond *et al.*, 1984) and these endings are further implicated in a recent study which compared two forms of surgery which differentially affect the musculotendinous region (Steinbach *et al.*, 1987a). In the marginal myotomy procedure, a surgeon first crushes and then makes cuts in the musculotendinous region whereas in a recession procedure, this site is not touched and the surgery is carried out exclusively in tendon. Open-loop pointing responses taken before and after the surgery indicate that the myotomy procedure is more deafferenting than the recession procedure.

Development

We are all convinced that appropriate binocular retinal stimulation must be present from birth in order to develop normal visual functioning (see e.g. reviews by Movshon and Van Sluyters, 1981; Boothe *et al.*, 1985). How important are eye movements to the developmental process? Hebb (1949) predicted that motility was crucial but it took another 30 years for the evidence to arrive. It is now clear that for maintenance of binocular interaction, the development of orientation selectivity, or normal visuomotor activity, motility is critical (see e.g. reviews by Buisseret, 1979; Hein and Diamond, 1983; Fregnac and Imbert, 1984). It has further been demonstrated by studies which compare proprioceptive deafferentation with reductions of ocular motility itself, that ophthalmic nerve afference affects the cortical development (Gary-Bobo *et al.*, 1986).

It is not clear what the proprioceptive signal provides in this situation, i.e. whether the necessary information is about the position of the eye in the orbit or whether it merely provides some form of "gating" signal that allows the retinal afference to be properly integrated (Fregnac

and Imbert, 1984). Kato (cited by Eggers, 1982) reported dramatic changes in horizontal rectus muscle fiber counts between neonates and adult humans. The lateral rectus count decreased from about 35,000 fibres to 23,000 while the medial rectus increased from 29,000 to 46,000 fibres in the adult and neonate respectively. Another study cited by Eggers (Goldschmidt) showed no change in the medial rectus counts but a similar decrease in lateral rectus fibres. These studies must be repeated because there is a possibility that fibres do not run the whole length of the muscle (McNeer and Spencer, 1982) which means a sampling artifact could influence the differences reported. The results are provocative however, because the largest age-related fiber count differences seem to be in the horizontal recti, implicating changes limited to the binocular alignment system. This suggests a parallel cortical and peripheral (musculature) tuning of the vergence system, one that we know is completed by an early age in humans (Held, 1985). How this would occur remains to be investigated.

Depth perception, vergence and other binocular functions

The studies cited above indicate that proprioception is required for the normal development of binocular interaction (as indicated by the development of ocular dominance columns in the cortex). This suggests that proprioception should be involved at a behavioral level in some binocular functions. Fiorentini *et al.* (1985) initially showed impairment of depth discrimination in adult cats who were proprioceptively deafferented by severing the ophthalmic nerve. They used a jumping stand technique to show this so the results could have been due to other deficits associated with orienting behaviors (e.g. impaired eye-head coordination). In a subsequent study Fiorentini *et al.* (1986), using an operant conditioning paradigm to eliminate the objections associated with the jumping stand technique, found markedly reduced stereoacuties in the deafferented cats. The surgery did not produce any observable strabismus but only small vergence errors are needed to diminish stereoacuity. While their stimulus conditions suggest that these were not likely to play a role in their findings, altered vergence responses have been found in deafferented monkeys (Guthrie *et al.*, 1982). It is more likely that eye position information, which is critical for correct scaling of vergence and hence disparity

values (Ono and Comerford, 1975) had been disrupted by the deafferentation. Consistent with this finding is Steinbach's (1986b) report of an alteration of eye position information following disruption of binocular vision in a single patient with ophthalmic section of the trigeminal nerve.

Mitsui (1986) and his collaborators have implicated proprioception in the etiology of strabismus. A major finding is that passive manipulation of the position of the non-deviating eye of exotropes causes a temporary alignment of the deviating eye (the "magician's forceps phenomenon"). This is not a "traditional" stretch reflex because the latency of response is too long. This effect can be demonstrated under general anesthesia; there is also electromyographic confirmation, with eye muscle innervation in one orbit being influenced by passive rotation of the other eye (Tamura and Mitsui, 1986). Kommerell (1984) has suggested caution in the interpretation of these results because of the unstable nature of EMG recordings and the long latencies involved in demonstrating the effect.

Temporal relationships

Skavenski's research indicates that there can be a crude inflow signal about eye position that is submerged when there is a conflict with outflow (Skavenski *et al.*, 1972). This would seem to indicate that inflow is a weak signal. Consistent with this is Evert's (1981) reminder that Sherrington described the effects of proprioception as "mild". Perhaps proprioception needs time and/or multiple presentations in order to have any effect. Are these important variables missing in studies that only support outflow? Ludvigh (1952) was the first to suggest that inflow may play a long-term role in the maintenance of oculomotor control. He called it "parametric adjustment" and assumed it to be a low level, unconscious modification of muscle function based on changes in, for example, metabolic states of the muscle. Since then, others have championed this argument (e.g. Carpenter, 1977; Steinbach, 1986b) and it has been incorporated into a model of adaptive compensation for changes in the oculomotor plant (Grossberg, 1986). There is indirect evidence that supports this notion of inflow as a slow calibrator of eye position.

Steinbach *et al.* (1987b) compared spatial localization in patients before and after surgical removal of an eye (enucleation). Shifts mea-

sured using the non-operated eye of a strabismic have been reported (Steinbach and Smith, 1981; Steinbach *et al.*, 1987a) and normals also use the positions of both eyes to specify visual direction, even if only one eye is seeing (Ono and Weber, 1981). It is not surprising therefore that removing an eye would disrupt egocentric localization. There were indications in the data from enucleates that the changes were slow acting, requiring a period of days to reach a maximum. These slow recalibrations, with time constants measured in days, also appear in studies of patients with sudden onset paralysis of the eye muscles (see e.g. Leigh and Zee, 1983, for summaries). A study of a monkey's adaptation to the changes in saccade amplitude following sectioning (tenectomy) of the attachments of the medial and lateral rectus muscles documents these slow changes and shows an additional finding of particular interest here. Snow *et al.* (1985) presented but did not comment on data that suggested that, immediately following the tenectomy, the non-operated eye's saccade amplitudes paralleled the changes in gain made by the operated eye, even while the operated eye was patched. A non-visual, presumably proprioceptive, signal appeared to be influencing the movements of the seeing eye.

Steinbach *et al.* (1987b) have analyzed the nature of the changes in localization following either strabismus or enucleation surgery and found that only the constant error changes over the days of post-operative testing. Variable error, indicated by the standard deviation of pointing responses, remained virtually the same in all these studies. This indicates that the underlying proprioceptive signal is not a rapidly changing one. It also suggests a *rapprochement* between the outflow and inflow positions that has inflow as the long-term calibrator of position from which outflow reads out instantaneous measures of eye position. The many demonstrations of the efficacy of outflow, e.g. the eye-press experiments (e.g. Stark and Bridgeman, 1983; Steinbach and Skarf, 1985), might show adjustments to the passive displacement of the eye if the eye were held in its new position for hour or days, rather than seconds.

CONCLUSIONS

Proprioceptive information about eye position is available from a variety of known receptors in the eye muscles and tendons. There is a possibility that the retrobulbar fascia (a very

complicated set of structures, see Koorneef, 1977) or other periorbital structures (e.g. local signs from tactile receptors on the cornea; Mark and Maurice, 1977) contain receptors that may also inform the brain about the orientation of the eye in its orbit. The presence of other afferents is clearly indicated by the oculocardiac reflex (Milot *et al.*, 1983) and the pain accompanying eye movements in retrobulbar neuritis (Havener, 1984).

The human undergoing surgical manipulation of the eye muscles or having some conditions that alters inflow (e.g. the herpes zoster patient or the patient with trigeminal neuralgia (Campos *et al.*, 1986; Mitsui, 1986; Steinbach, 1986a, b) may provide instructive findings. Another useful patient to study may be the one having the extraocular muscles temporarily paralyzed by botulinum toxin (Scott, 1980). Physiological investigators are hampered by the relative inaccessibility of the afferent pathways and the difficulty in extrapolating the effects of passive stretch to the normal situation in which extra- and intra-fusal fibres are jointly activated. If scientists are sufficiently convinced that there is an important role for afference, then these difficulties will be overcome.

In a general consideration of the function of skeletal muscle spindles, Clark and Horch (1986) traced the remarkable reversals in thinking about whether position sense could be derived from their responses. We are far from understanding proprioception in skeletal systems. The suggestions recently made for the combined monitoring of afferent and efferent signals about spindles (Matthews, 1982; McCloskey, 1981) to provide position information in skeletal muscles have their parallel amongst eye movement theorists. Matin (1976) and Shebilske (1977) have suggested that gamma-efferent and intrafusal afferent responses are both necessary to provide eye position information. If we come to understand the oculomotor system's use of afference, we may be able to understand its use in the skeletal system (Sivak, 1983).

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