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A framework for considering the role of afference and efference in the control and perception of ocular position

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Abstract. It has been well established that extra-retinal information is used in the perception of visual direction and distance. Furthermore, a number of studies have established that both efference copy and afferent discharge contribute to the extra-retinal signal. Despite this, no model currently exists to explain how the signals which arise through oculomotor control contribute to perception. This paper attempts to provide such a framework. The first part of the paper outlines the framework [the cyclopean equilibrium point (EP) model] and considers the binoculus or cyclopean eye from the perspective of a current account of motor control (the EP hypothesis). An existing model is used to describe how the nervous system could utilise available efference copy and afferent extra retinal signals when determining the direction and distance of cyclopean fixation. Although the cyclopean EP model is speculative, it allows for a parsimonious framework when considering the oculomotor contribution to perception. The model has the additional advantage of being consistent with current theories regarding the control and perception of limb movement. The second part of the paper shows that the model is biologically plausible, demonstrates the use of the proposed model in describing the central control of eye movements with regard to non-conjugate peripheral adaptation and reconciles seemingly disparate empirical findings.

1 Introduction

In humans (and many other animal species), vision is the primary sensory system used to provide information about object location which has the precision required for supporting skilled interaction with objects of interest. Human vision begins with the images of objects on the retinae, but knowledge of an image's retinal position is not sufficient for determining the location of a particular object with respect to a hand or the body. Object localisation requires knowledge of ocular position with respect to the head, and head orientation with respect to the shoulders (see, e.g. Berthoz 1985). In this paper we will describe a model of the extra retinal contribution to perceiving the position of the eyes in the head, suggesting how both the control and the perception of eye position are based upon a single binocular system of coordinates (the *binoculus*, Hering 1868/1977, or *cyclopean eye*, Helmholtz 1894/1924).

1.1 The need for a framework

Since Hering proposed his law of equal innervation for the two eyes, it has been widely accepted that the eyes are controlled as a single 'organ'. It has also been shown that vergence and version (conjugate) eye movements are controlled somewhat independently and various models of the control processes underlying these movements have been proposed (e.g. Clark and Stark 1974; Robinson 1975, 1981; Tweed 1997). The form of the oculomotor control signals is not only important for understanding the generation of eye movements, it is also important for understanding the sensing of eye position and the state of vergence since these sensations involve a copy of the commands to the extra-ocular muscles (Bridgeman and Stark 1991). There has, however, been little attempt to provide a unified modelling framework for both the control and perception of ocular position.

The equilibrium point (EP) hypothesis for motor control provides an integrative and effective account of both neuromuscular control and limb position perception (see Bizzi et al. 1976; Feldman 1980, 1986; Feldman and Latash 1982; Houk 1979; Kelso 1977; Kelso and Holt 1980; Latash 1993; Polit and Bizzi 1978, 1979); although some of the details are the subject of debate,

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the general principles of this hypothesis are now generally accepted (Berkinblit et al. 1986; Bizzi et al. 1992; Feldman and Levin 1995; Latash 1993). Here the EP hypothesis is applied to the binocular horizontal eye movement system in a revision and extension of Feldman's (1981) earlier study of the EP control of horizontal saccades in a single eye.

The EP account of the control and perception of horizontal eye position developed here is necessarily speculative, but it serves a useful role in explaining how oculomotor control gives rise to extra-retinal sensation and, ultimately, to perception. The need for such a framework may be illustrated with regard to the role of vergence in distance perception: it is well established that the angle of ocular vergence provides the nervous system with information regarding egocentric distance (see Foley 1980; Tresilian and Mon-Williams 1998). Although the role of vergence in distance perception is well documented, a satisfactory explanation of how the nervous system 'senses' vergence angle is lacking. Von Hofsten (1976) has proposed that the nervous system is concerned with 'vergence effort'; this seems a reasonable suggestion but raises the question of *how* the sense of effort arises. The account we provide is fully consistent with all available data and thereby resolves a number of inconsistencies in the literature. It accounts for why the dynamics of convergence and divergence are different; why saccadic intrusions are often observed in off-midline shifts of vergence fixation; and why changes in efference copy *and* afferent feedback lead to alterations in perception. In the present article we restrict ourselves to a description of the modelling framework and therefore present a qualitative rather than quantitative account.

1.2 The proposed framework

Feldman (1981) used the EP hypothesis to describe how horizontal movements of a single eye might be controlled. We revise and extend these ideas to the binocular system and show how they relate to the perception of visual direction and distance; we refer to the scheme as the 'cyclopean EP model'. Attention is restricted to the horizontal meridian but similar principles are likely to apply to vertical movements of the eyes.

Horizontal movements of the two eyes may be considered as either conjugate, when the eyes move in the same direction, or disconjugate, when the eyes move in opposite directions. These two types of eye movement are commonly referred to as version and vergence movements, but we will use the term 'conjugate' rather than version. Eye movements of both classes are responsible for maintenance of static fixation (gaze holding), rapidly changing eye fixation position (saccadic movement) or continuously maintaining fixation on a moving object (pursuit). Hering (1868/1977) observed that many eye movements are conjugate from birth, even when one eye is covered. Hering argued that a common innervation must be sent to the eyes to achieve this conjugacy, implying that the two eyes are controlled as a single unit; we develop this idea using the EP hypothesis. We show how the perception of cyclopean visual direction and the control of the cyclopean eye are closely interrelated when the EP hypothesis is used as a framework.

Our scheme has several important features, some of which are shared with other models. The scheme adopts those features of other models which we believe to be necessary for a unified account of eye movement control and eye position perception. We will outline these features here in point form, with later sections providing a detailed explanation and justification:

1. The nervous system reduces by half the number of degrees of freedom which need to be controlled at a central level by specifying commands to a virtual 'cyclopean eye' via antagonistic muscle units.
2. During conjugate horizontal eye movements, the left lateral rectus and the right medial rectus work together as one functional unit (the left cyclopean muscle), with the left medial rectus and the right lateral rectus working together as an antagonistic functional unit (the right cyclopean muscle).
3. Following Feldman (1981), horizontal eye movements are controlled by programming shifts of the threshold lengths for active force development in the medial and lateral recti. Control of conjugate movement involves two commands: a 'reciprocal' command which controls eye position and a 'coactivation' command which controls eye stiffness.
4. A second command signal is involved in the production of vergence eye movements. This command is directed to the medial recti only and specifies equal changes of the threshold lengths of these two muscles. This command will be termed the *vergence command* but it is capable of accurate control of vergence movements only along or close to the midline. The vergence movements involved in changes of fixation distance away from the midline require both a vergence and a conjugate command.
5. The perception of ocular position depends upon efference copy and afferent feedback: afferent information is pooled from the two muscles within the functional cyclopean unit.
6. Information (both efference and afferent) from the two cyclopean muscles is summed to give rise to a neural signal approximating the cyclopean direction, and then differenced to give a signal approximating the cyclopean fixation distance (distance from the cyclopean eye to a fixated target).

In the next section ('The cyclopean EP model') we describe conceptually a simple model with these features which is capable of providing a unified account of the control and perception of horizontal ocular position. In the subsequent section ('Relating the model to experimental observations'), we describe a number of experiments and observations, both physiological and behavioural, which are consistent with the model and show how it accounts for, and unifies, a variety of disparate findings.

2 The cyclopean EP model

2.1 The EP hypothesis

As the EP hypothesis is central to the model, we will provide a brief account of it here. A basic idea of the EP hypothesis is that static limb posture is an equilibrium between external loads (including gravitational loads of the limb segments themselves) and muscular forces; movement is considered to be the transition between postures effected by shifting the EP. Feldman (1966, 1986) proposed that movement control is achieved by central commands which shift the EP by changing the muscle lengths at which autogenic tonic α-mononeuton (MN) recruitment begins. These threshold muscle lengths are denoted by the symbol λ. When a monoarticular muscle's moment arm is constant with changes in joint angle, muscle length (L) and joint angle (θ) will be related by a simple linear relationship and so we can talk about the threshold angle (β) for MN recruitment instead of the threshold length (λ). The static force (or torque, T) developed by a muscle is then a function of how much longer it is than its centrally determined threshold length:

$$T = f(\theta - \beta) \tag{1}$$

Example static force-length (F-L, or torque-angle) characteristics of intact muscle are shown schematically in Fig. 1 (the characteristics shown are schematic of those derived from human horizontal recti). These characteristically intersect the ordinate (generate zero active force) at a point determined by the current level of central command. As the command varies, the characteristics shift along the ordinate but remain similar in shape. The F-L characteristics of the horizontal recti are linear except at low force levels (Collins et al. 1975; Robinson et al. 1969) and ignoring the non-linear 'toe' region has been found to have little effect on simulations (e.g. Clark and Stark 1974; Dean 1996). Thus, to a good approximation, the F-L characteristics of horizontal recti can be treated as linear, i.e.

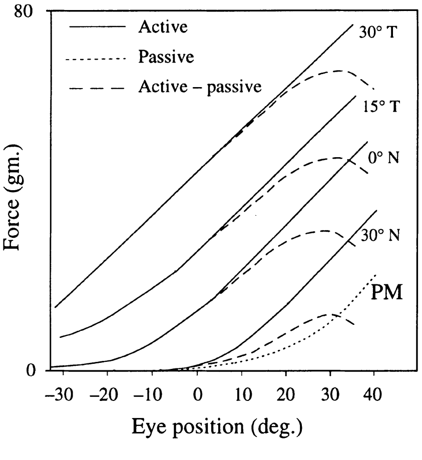

Fig. 1. Schematic of the empirically observed force-length (F-L) characteristics of human horizontal recti in vivo based on the results of Collins et al. (1975) and Robinson et al. (1969) (similar results were observed for both lateral and medial recti). Muscle tension in gram force units is plotted as a function of eye position in degrees for levels of central innervation which were assumed constant. This assumption is based on Hering's law and follows from the fact that fixation was constant in the unmeasured eye during the experiment. The F-L characteristics for several different directions of gaze (levels of central innervation) are shown: 30 deg Nasal (N, –ve), 0 deg (primary position), 15 and 30 deg Temporal (T, +ve). The *solid curves* indicate the measured F-L characteristics. The *dotted curve* is the characteristics of passive muscle (*PM*). The *dashed curves* are the difference between the F-L characteristics and the passive characteristic and indicate the active component of the F-L characteristics

$$T = k[\phi - \beta]^+ \tag{2}$$

where ϕ is the gaze angle, k is a constant stiffness and the notation $[x]^+$ means max(0, x).

Feldman's formulation of the EP hypothesis identifies the threshold length for active force development with the threshold for α-MN recruitment which is, in turn, identified as the threshold of the autogenic tonic stretch reflex mechanisms (Feldman 1986; Latash 1993). It is generally accepted that extra-ocular muscles lack any autogenic stretch reflexes (Carpenter 1988; Keller and Robinson 1971; Robinson 1981). Despite this general acceptance, the absence of a low-gain tonic stretch reflex mechanism in human extra-ocular muscles has not been established (see below for discussion). Irrespective of whether or not reflex mechanisms are present, human extra-ocular muscle static F-L characteristics have the form shown in Fig. 1 (Collins et al. 1975; Robinson et al. 1969) as required by Feldman's version of the EP hypothesis. If the extra-ocular muscle lacks stretch reflexes, then the observed F-L characteristics are implemented by the mechanical properties of these muscles (Robinson et al. 1969). If reflex mechanisms are present, then the observed F-L characteristics reflect the operation of these reflexes, as in other skeletal muscle (Nichols and Houk 1976). In either case, the EP formalisation describes the overall behaviour of the system (Eq. 1). However, the threshold length for active force development (see Fig. 1) is not the threshold length for α-MN recruitment if the muscle lacks reflexes. If the muscle giving rise to the F-L characteristics in Fig. 1 lacks reflexes, then its level of activation is constant for any given characteristic. The muscle starts developing significant active force when it is longer than its threshold length for the current level of activation; if it is shorter than this length it generates negligible active force. The level of activation for a muscle which lacks reflexes determines the threshold length for active force development. Equation 1 (or Eq. 2) describes the static F-L characteristics of Fig. 1 (irrespective of whether the muscles are reflex equipped or not).

Joints are typically controlled by at least two muscle groups, flexors and extensors. To flex a joint the flexor torque must be greater than the extensor torque and vice versa for extension. If these torques are simultaneously increased by the same amount, the joint will not change position but will instead become stiffer. Feldman (1980) has proposed that joint position and stiffness are controlled separately by two central commands, a reciprocal (R) command and a coactivation (C) command, respectively. For a joint controlled by a single flexor and extensor muscle, the R and C commands are related to individual muscle threshold angles (or lengths) as follows:

$$R = 1/2(\beta_{\mathrm{fl}} + \beta_{\mathrm{ext}}) \qquad C = 1/2(\beta_{\mathrm{fl}} + \beta_{\mathrm{ext}}), \tag{3}$$

Where βfl and βext are the threshold angles for active force development in the flexor and extensor, respectively. This formulation was devised by Feldman under the assumption that muscles are reflex equipped. In the absence of reflexes a slight modification is required: threshold angles (β) must be replaced with variables describing the neural excitation level associated with the threshold angles. Neural excitation (N) and threshold angle (β) are in one-to-one correspondence such that $\beta = n(N)$ and hence $N = n^{-1}(\beta)$. Thus, in the absence of reflexes in the extra-ocular muscles, Eq. 3 should read

$$R = 1/2[n^{-1}(\beta_{\mathrm{fl}}) + n^{-1}(\beta_{\mathrm{ext}})]$$
$$C = 1/2[n^{-1}(\beta_{\mathrm{fl}}) - n^{-1}(\beta_{\mathrm{ext}})] \tag{4}$$

If a linear functional form for n^{-1} is assumed ($N = N_0 + m\beta, \quad N_0 = n^{-1}[0]$) – which is simply to assume that changes in β are proportional to changes in N – Eq. 4 simplifies to

$$R = N_0 + m(\beta_{\mathrm{fl}} + \beta_{\mathrm{ext}})/2 \qquad C = m(\beta_{\mathrm{fl}} - \beta_{\mathrm{ext}})/2 \tag{5}$$

These concepts are sufficient for stating our model of eye movement control.

2.2 Control of conjugate eye movements

As already stated, we suppose that the central nervous system (CNS) is concerned with controlling the position of a virtual cyclopean eye. The cyclopean eye has two opposing 'virtual' muscles for horizontal movements: the left and right cyclopean muscles (Fig. 2, left). We suppose that the CNS specifies a reciprocal and coactivative command for the cyclopean eye (R_c and C_c). The R_c command is responsible for changes in gaze angle while the C_c command is responsible for changes in the stiffness of the eye's position in the orbit (which determines the stability of cyclopean gaze direction). These commands would then be translated into muscle commands at a lower level (Fig. 2. left).

The scheme is illustrated diagrammatically in Fig. 3 (example A, columns 1 and 2) for a pure conjugate saccade with the eyes parallel. The top two rows of column A show the R_c and C_c commands and a vergence (V) command (the latter being zero – eyes parallel, no vergence). It is evident that the eyes need no dynamic load stabilization and that a saccade needs to be (to a first approximation) as fast as possible. The results of Robinson et al. (1969) and Collins et al. (1975) have demonstrated considerable coactivation during fixation. Feldman (1981) pointed out that coactivation is likely to be useful in saccadic eye movements to avoid oscillations when the eye arrives at its equilibrium position. In order that saccades are as fast as possible, the C_c command should drop to zero during movement. It may therefore be proposed that the level of coactivation starts at a non-zero value, drops to zero during the saccade and then increases again to a non-zero level as the eye approaches its new position (this is shown schematically in Fig. 3, second row). The R_c command shown for saccades (Fig. 3, top) differs from the R command originally proposed by Feldman (1981). Feldman's general approach is to assume that the central commands are monotonic (ramp) shifts and that the characteristic burst pattern of the electromyogram (EMG) is a result of the interaction of central commands and reflexes (Feldman and Levin 1995). There are two reasons to suppose that this cannot be the case for eye movements. First, there may be no reflex mechanism as previously discussed. Second, it has been established that the burst pattern of ocular MNs (OMNs) is generated more centrally (by brainstem structures) rather than by the OMNs themselves as predicted by Feldman's model (see, e.g. Fuchs et al. 1985; Robinson 1981; Scudder 1988). The burst-tonic pattern of agonist OMN activity seen during saccades is necessary to overcome the over damped passive dynamics of the oculomotor plant (see, e.g. Robinson 1981). For these reasons the R_c command is shown in Fig. 3 as having a burst-tonic pattern.

Rows 3–5 in Fig. 3 (column A) show the shifts in the virtual threshold lengths or angles of the virtual cyclopean muscles. From Eq. 1, these may be assumed to be given by

$$\beta_{\mathrm{R}} = R_c - C_c \qquad \beta_{\mathrm{L}} = R_c - C_c \tag{6}$$

where β_{R} and β_{L} are the threshold angles for the right and left cyclopean muscles, respectively. We propose that the medial and lateral recti which compose the left and right cyclopean muscles receive identical commands such that $\beta_{\mathrm{L}} = \beta_{\mathrm{RM}} = \beta_{\mathrm{LL}}$ and $\beta_{\mathrm{R}} = \beta_{\mathrm{LM}} = \beta_{\mathrm{RL}}$, where β_{LM} and β_{RM} are the threshold angles for force development in the left and right medial recti, and β_{LL} and β_{RL} are the same for the lateral recti (this obeys Hering's law of equal innervation). These thresholds need to be converted into neural excitations if there are no stretch reflex mechanisms, according to $N = N_0 + m\beta$ (assuming N and β are in direct proportion, see above). For example, considering only one eye (the left):

$$R_c + C_c = \beta_{\mathrm{L}} = \beta_{\mathrm{LL}} \longrightarrow N_{0,\mathrm{L}} + m_L\beta_{\mathrm{LL}}$$
$$R_c - C_c = \beta_{\mathrm{R}} = \beta_{\mathrm{LM}} \longrightarrow N_{0,\mathrm{L}} + m_{\mathrm{L}}\beta_{\mathrm{LM}}$$

Figure 3A (rows 7 and 8) shows the neural excitation for the recti of the left eye, which can be considered as constituting the descending inputs to the OMN pools and will directly determine the EMG in the absence of a stretch reflex (rows 8 and 9). This is the EMG pattern typically observed empirically during saccades (see, for example, Carpenter 1988 for review).

2.3 Control of vergence movements

We propose that vergence movements involve a command (V) to the left and right medial recti only (see Fig. 2, left). These two muscles can be considered a single virtual muscle (the vergence muscle). The V command alone is responsible for changes in vergence along the midline involving symmetrical movements of the two eyes. In our scheme, changes in vergence away

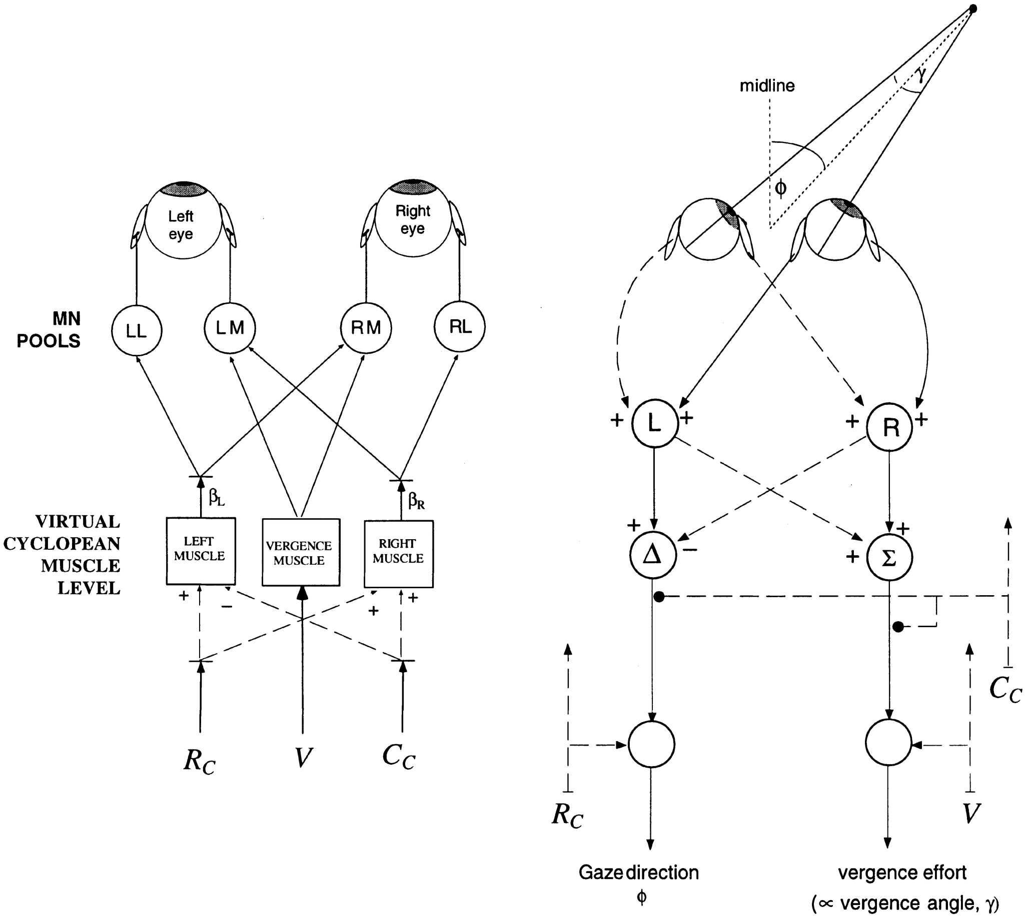

Fig. 2. Schematic providing a detailed illustration of the basic concepts of the cyclopean equilibrium point (EP) model. *Left*: levels of control. The reciprocal (R_c) and coactivation (C_c) commands for the virtual cyclopean eye are first split into specific commands to the virtual cyclopean muscles according to $\beta_R = R_C + C_C$ and $\beta_L = R_C - C_C$. The medial recti (*M*) and lateral recti (*L*) which compose the left and right cyclopean muscles receive identical commands to their respective motoneuron pools (labelled *LL*, *LM*, *RM*, *RL*) according to the rule $\beta_L = \beta_{RM} = \beta_{LL}$ and $\beta_R = \beta_{LM} = \beta_{RL}$ where, β_{LM} and β_{RM} are the threshold angles for force development in the left and right medial recti, and β_{LL} and β_{RL} are the same for the lateral recti. This scheme obeys Hering's law of equal innervation. The vergence command is the same to both medial recti (again obeying Hering's law). *Right*: schematic of stages in the computation of signals proportional to gaze direction (ϕ) and vergence angle (γ). Afferent activity in each virtual cyclopean muscle is computed as the average of the activity of the two extra-ocular muscles which comprise them. The sum ($\sum$) and difference (Δ) of this averaged activity is then computed. The sum is used in combination with efference copy of the vergence command (and possibly the conjugate coactivation command) as information about vergence effort. The difference is used (together with efference copy of the conjugate command) as information about gaze direction

from the mid line (those involving asymmetrical eye movements) require a simultaneous conjugate R_c command for their production. We would therefore expect to observe more saccadic intrusions when making off-midline vergence movements. This expectation is confirmed in the literature (e.g. Erkelens et al. 1989a; Ono and Nakamizo 1978), as we discuss later.

The vergence command is the same to both medial recti (Hering's law) and is simply superimposed upon the conjugate command: vergence and conjugate commands to the medial recti are additive. A consequence of this is that increasing convergence is opposed by the lateral recti: as the medial recti shorten so the lateral recti will lengthen, stretching them beyond their threshold lengths and causing them to develop an active force in opposition to the stretch. For this reason, a given vergence command will need to take into account the current conjugate commands if the desired vergence angle is to be achieved and vice versa. We are grateful to an anonymous reviewer for drawing our intention to the fact that Hering (1868/1977) assumed that conjugate and vergence commands sum at the eyes whilst others have believed that the commands are summed prior to the final central command being sent. According to our scheme, the commands are summed at the level of the OMN pools. Figure 3 (example B, columns 3 and 4) shows a schematic of the separate conjugate and vergence commands (top) and how these combine at the OMN level to specify the threshold angles (β) in the medial and lateral recti (Fig. 3 column B, rows 6 and 7).

The suggestion that the vergence command is directed only at the medial recti implies that, during convergence, contraction of the medial recti will tend to stretch the lateral recti, causing the latter to develop a tension opposing this stretch (the lateral recti oppose convergent movement). This is in contrast to divergent movements,

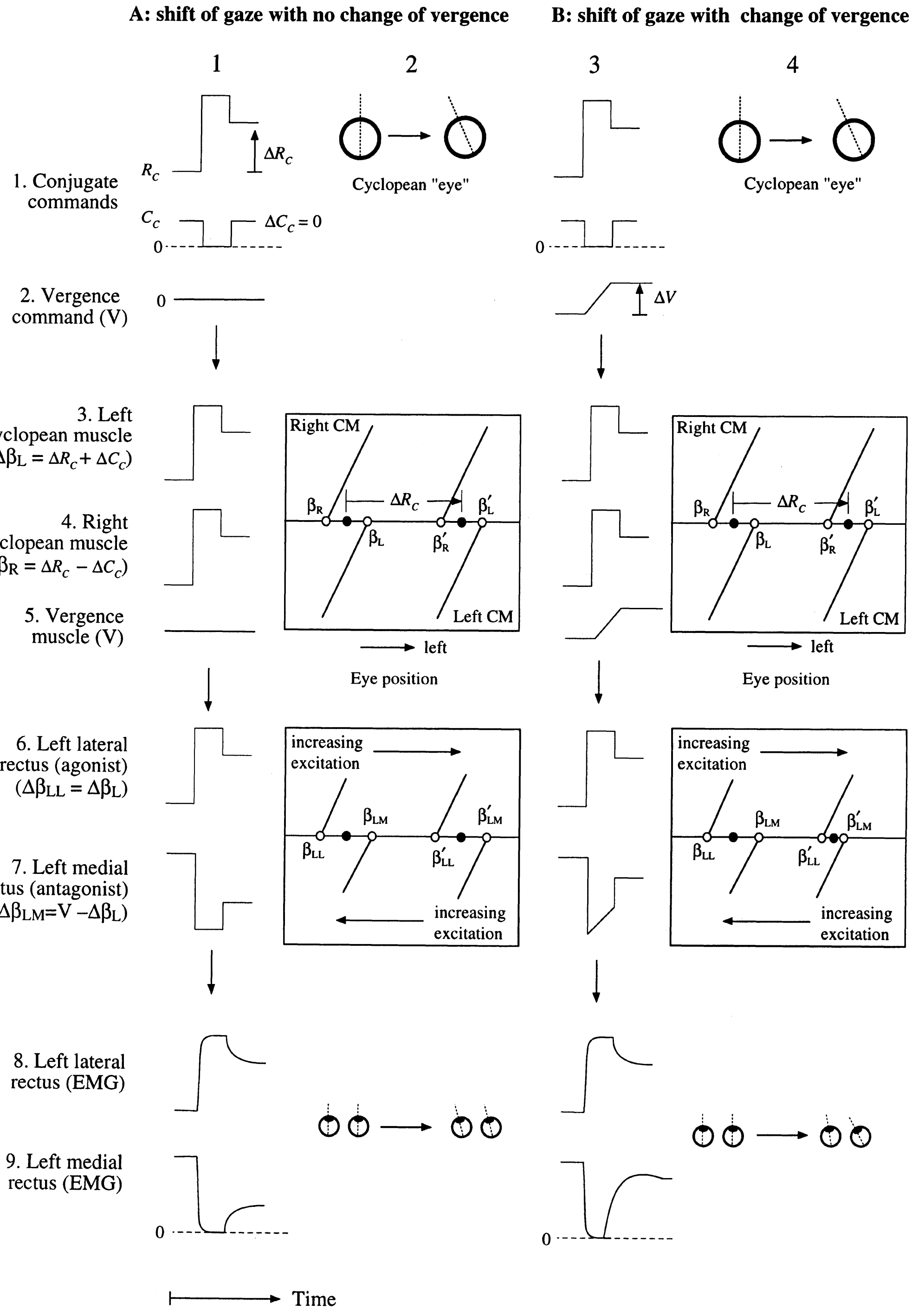

Fig. 3. Schematic illustration of the EP control scheme for eye movements developed in the text. *Columns 1 and 2* refer to example **A** (a shift of gaze direction from straight ahead to the left with the eyes parallel – no vergence). *Columns 3 and 4* refer to example **B** (a leftward shift of gaze direction with a simultaneous convergence movement). *Columns 1 and 3* show schematic representations of the control signals at each level of the model. *Columns 2 and 4* indicate schematically the initial and final mechanical states resulting from the control signals. In the insets (*columns 2 and 4*), the *unfilled circles* indicate the threshold eye position of a muscle; *filled circles* indicate the equilibrium position of the eye when the muscles have the threshold positions indicated by the unfilled circles. *Rows 1 and 2* show simplified schematics of control at the level of the cyclopean eye. *Rows 3–5* show the behavior of the hypothetical 'virtual' cyclopean muscles (*CMs*) in response to the commands in rows 1 and 2. The threshold positions of the left and right CMs begin at β_L and β_R, respectively, and shift in response to ΔR_C to β'_L and β'_R ($\Delta\beta$, there is no net shift in C_c in these examples). *Rows 6 and 7* show the command inputs to the horizontal recti ocular motoneurons (OMNs) for one of the two eyes (the left, see text for details). *Rows 8 and 9* illustrate the form of the EMG signals from the left horizontal recti expected from the OMN input signals shown in rows 6 and 7 assuming the muscles have no stretch reflexes. The change in position of the two eyes is shown schematically in the corresponding position in columns 2 and 4

where the lateral recti are the prime movers and cause the eyes to turn outwards. Thus, the lateral recti cause divergence but they do this 'passively' in that they receive no command: control of divergence can only be achieved by controlled relaxation of the medial recti. For this reason, we would expect convergent and divergent eye movement dynamics to be different and discuss evidence that this is the case in the second part of this paper. According to this conception of vergence control, there can be no vergence coactivation command per se, and the eyes will move until the forces exerted by the medial and lateral recti are balanced. It will be noted that the medial recti shorten owing to a command to increase vergence in changes along the midline so that the lateral recti are stretched beyond their threshold lengths (determined by the R_c command). This causes the muscles to develop active force and resist further stretch. Thus, both the medial and lateral recti are actively increasing the eye's positional stiffness, thereby reducing the potential oscillations which might otherwise arise owing to the absence of a coactivation command. Erkelens et al. (1989c) have, however, reported end-point oscillations during changes in vergence along the midline, suggesting that under these conditions the stiffness may reduce end-point oscillations but is not sufficient to damp them out completely.

2.4 Two roles for afferent feedback?

Human extra-ocular muscle has a wealth of afferent organs (e.g.; Gentle and Ruskell 1997; Ruskell 1978, 1989) and it seems reasonable to suggest that: 'such an elaborate physiological system should have a functional role' (Bridgeman and Stark 1991, p. 1904). In Feldman's version of the EP hypothesis, afferent feedback plays a basic role in normal motor control since the mechanism of control is to change the threshold of the tonic stretch reflex. It is accepted that there is no stretch reflex in extra-ocular muscle and this is based largely on results reported by Keller and Robinson (1971), which showed that there is no stretch reflex in the extra-ocular muscles of the rhesus monkey (*Mucaca mulatta*). These results do not establish the absence of a tonic stretch reflex in human extra-ocular muscle. It is known that the afferentation of extra-ocular muscles is rather species specific (see, e.g. Spencer and Keller 1991). The rhesus monkey possesses numerous myotendinous cylinders (MTCs) which are also present in man (Gentle and Ruskell 1997; Ruskell 1978), but lacks spindles which are found in human extra-ocular muscles (Cooper and Daniel 1949; Ruskell 1989). Ruskell (1978) found that all the muscle fibres contributing to MTCs were non-twitch fibres, which presumably generate tonic rather than phasic contractions (Lewis and Zee 1993; Peachy 1971). Furthermore, passive movements of the eye muscles appear to be a relatively weak stimulus for MTC activation (Lewis and Zee 1993; Ruskell 1978). Given these findings, the experimental procedures of Keller and Robinson (1971) might not be expected to yield significant changes in OMN firing rates even if a tonic stretch reflex were present; muscle stretches were obtained by passive movement of the eye and recordings were restricted to large OMNs associated with fast twitch fibres. As Keller and Robinson acknowledged, their results do not rule out the possibility of stretch reflexes involving only slow fibres and these would be the primary candidate fibres for finding a tonic stretch reflex. It may be concluded that, in man, a low-gain, tonic stretch reflex involving the slower motor units remains a possibility. It must be accepted, however, that there is little direct evidence to support this possibility and the evidence that does exist is far from conclusive.

It is possible that extra-ocular afference is used to determine eye position for the purposes of perception and such a role is independent of the existence of a stretch reflex. Eye position information is required if visual information is to be transformed from a retinocentric coordinate system into the body centred coordinate systems used to control movements of the body in normal action (Flanders and Soechting 1990). It also appears that eye position information can play a role in the perception of distance (Foley 1980; Tresilian and Mon-Williams 1998). These perceptual issues are independent of whether afference plays a role in eye movement control via a stretch reflex mechanism. Controversy once existed over whether afferent signals are used in the determination of ocular position. In theory, efference together with retinal image feedback could provide sufficient information for the CNS to determine cyclopean direction. The following empirical findings strongly suggest, however, that ocular proprioception is used in the perception of eye position:

1. Ocular proprioception influences the perception of visual direction (Bridgeman and Stark 1991; Gauthier et al. 1990; Roll et al. 1991).
2. Ocular proprioception affects the processing of visual information (e.g. Lal and Friedlander 1989).
3. Trigeminal-oculomotor synkinesis results in abnormal spatial localisation (Lewis and Zee 1993).
4. Abnormal sensory function of the trigeminal nerve results in abnormal spatial localisation (Campos et al. 1986).
5. Abnormal spatial localisation occurs if the extra-ocular musculature are externally vibrated (Velay et al. 1994).
6. Spatial localisation can be reasonably accurate immediately following surgery for strabismus even in the absence of visual information (Steinbach and Smith 1981).

We now consider the role of afferent signals in the perception of ocular position. In the EP hypothesis, both afference and efference are usually necessary for the accurate (kinaesthetic) perception of joint position (Feldman and Latash 1982). A variety of experimental data supports the notion that efference copy and afferent signals are used for joint position perception (e.g. Feldman and Latash 1982; McCloskey 1978; Rymer and D'Almeida 1980). Here we use the EP hypothesis to provide an account of eye position perception; we deal first with perception of visual direction and then with the perception of distance via vergence angle.

2.5 The perception of visual direction and fixation distance

According to the EP hypothesis, joint position perception must, in general, involve both an afferent and an efferent component. For a static joint position the active muscle torque (T_A) exerted at the joint by a given muscle is a monotonically increasing function of $(\theta - \beta)$, the difference between the joint angle (θ) and the threshold angle for force development (β). If the joint angle is less than or equal to the threshold angle, there will be no active muscle torque. Thus, only if the muscle is loaded will there be an active torque; in the absence of load the muscle will be in equilibrium when $\theta = \beta$. The two central commands mutually determine the threshold angle β (see Eq. 3 above). The effect of the coactivation command is to change the slope of the torque-angle characteristic of the joint; the effect of the reciprocal command is to shift the torque-angle characteristic. The total muscle torque (T) can be written

$$T = T_A + T_P = f_C(\theta - R) \tag{7}$$

where T_P is the passive muscle torque when $\theta = R$ and f_C is an increasing function of $(\theta - R)$ dependent upon the level of coactivation (Feldman and Latash 1982). The F-L characteristics of the horizontal recti are, to a good approximation, linear (Eq. 2) which means that Eq. 7 can be written

$$T = K_c(\phi - R_c), \tag{8}$$

where K_c is the (horizontal) stiffness of the eye in the orbit which is a function of the C_c command. One can invert Eq. 8 to obtain an expression for joint angle:

$$\phi = R_c + T/K_c \tag{9}$$

This equation shows that eye position is a function of central commands and muscle torque (T). From this it follows that the joint angle must generally involve both efference copy and afferent information (about the joint torque, Feldman and Latash, 1982). It is clear from Eq. 9 that the value of the reciprocal command provides a zero or reference point in the measurement of eye position since $\phi = R_c$ in the absence of torque. The value of the coactivation command is used in transforming torque information into angular units and can thus be considered to be involved in the determination of a scale for the measurement of the joint angle.

When there is no external load on a muscle the joint angle will be determined by the value of the reciprocal central command. In such circumstances, afferent information is not required for accurate joint angle perception. When viewing objects at optical infinity, the eyes may approximate these conditions since they are not subject to significant gravitational loads from either the mass of the globe itself or from the mass of other bodies (any small static loadings that do exist are essentially unchanging). Eye position will be specified by the value of the R_c command. This means that efference copy information may be sufficient for the perception of ocular position when fixating targets at optical infinity. This notion is in agreement with Helmholtz's (1894/1924) proposal: a copy of the R_c command is sufficient for perceiving gaze direction (the direction the cyclopean eye is pointing).

If loadings are introduced, then the situation will change and ocular position will, by Eq. 9, be specified by both afference and efference. This has been confirmed using several methods of applying external loadings (Bridgeman and Stark 1991; Gauthier et al. 1990; Velay et al. 1994). Loadings will also be introduced by vergence eye movements as these move the eyes from the positions specified by the R_c command. For vergence along the midline (produced by a pure vergence command) an efference copy of the R_c command is still sufficient to specify cyclopean gaze direction. For changes in fixation distance away from the midline, a conjugate command is implicated in addition to a vergence command. In the latter condition, the two targets can lie along the same cyclopean direction, differing only in their radial distances along this direction. The additional conjugate command required to change fixation distance along an axis away from the midline means that the cyclopean direction of the target cannot, in general, be recovered from a conjugate efference copy in the presence of vergence. Additional information is therefore necessary to determine cyclopean direction and this can be obtained from afference. When there is vergence, the tension in the medial recti loads the lateral recti, causing these to be stretched beyond their threshold lengths, thereby generating an afferent signal. We propose that the afferent activity generated in the presence of vergence is used in the perception of both cyclopean direction and vergence angle, the latter being used for the perception of fixation distance. For this reason, our scheme differs from those which propose that these perceptions can be derived from efference alone (e.g. Greve et al. 1993).

Our scheme is illustrated in Fig. 2 (right). In a first step, afferent activity from the right medial rectus and left lateral rectus (comprising the left virtual cyclopean muscle) is averaged. A similar process occurs for the two muscles comprising the right cyclopean muscle. This first step provides a measure of the afference associated with the two virtual cyclopean muscles. In a second step, the sum and difference of the cyclopean muscle afferences are computed. Following this step, the cyclopean gaze direction is computed by transforming (based on the current level of the C_c command) the differenced afference signal and adding it to a copy of the R_c command. For vergence along the midline, the differenced afference will be zero, in which case a copy of the R_c command specifies gaze direction. The sum of the cyclopean afferent signal is in one-to-one correspondence with the amount of convergent torque (which can be equated with the vergence effort, cf. Feldman and Latash 1982). Because of this relationship between torque and the summed cyclopean afference, the latter quantity is a function of vergence angle and can therefore be used in the perception of fixation distance.

3. Relating the model to experimental observations

3.1 The physiological evidence for the model

One crucial requirement of any model of extra-ocular control and perception is that it is biologically plausible. A number of studies have established that the equilibrium point hypothesis is compatible with our current knowledge of neurophysiological mechanisms (see, for example, Feldman and Latash 1982). There is also reasonable evidence that the nervous system is arranged to control functional pairs of muscles from the two eyes (Moschovakis et al. 1990; Nakayama 1975). Feldman (1981) has shown that data collected by Collins et al. (1975) are consistent with the notion that a reciprocal and a coactivation command are initiated during horizontal eye movements. It therefore appears that the general arrangement of the cyclopean EP model is physiologically plausible. We have already discussed the neurophysiological evidence for functional afferentation of the extra-ocular muscles and we will now review the neurophysiological basis for some more specific features of the model.

3.2 The vergence command is only directed at the medial recti

The most controversial aspect of the cyclopean EP model may be the fact that the vergence command is supposed to drive only the medial recti. The proposition has no direct physiological evidence for or against it (the neural pathways for vergence are poorly defined), but we will produce indirect evidence that seems to provide some support for this notion.

Mays (1984) has shown that convergence cells (cells that fire in response to convergence) are found in the mesencephalic reticular formation. The convergence cells have a linear relationship with the vergence angle, do not fire during conjugate movements, temporally lead the vergence angle and have a firing pattern that closely couples the motoneurons of the medial rectus. The vergence cells found by Mays were all close to the medial rectus motoneurons, which is the ideal location for cells that primarily project to the medial recti. Schiller (1970) has also observed cells specifically related to vergence in the oculomotor nuclear complex (which projects to the medial recti). Gamlin and Mays (1992) have reported that medial recti motoneurons in the oculomotor nucleus discharge in a manner related to the position and velocity of ocular position during vergence movements. In contrast, divergence cells are sparse and, moreover, their activity appears to be only weakly correlated to vergence (Mays 1984). Judge and Cumming (1986) also found vergence cells that increased their firing primarily during convergence rather than divergence movement.

In contrast to these more recent studies, Keller and Robinson (1972) and Keller (1973) did not find OMNs which were specific to vergence. Keller and Robinson (1972) also found activity in the abducens nuclei (which contain MNs innervating the lateral recti) during vergence movements. Such activity in the abducens is predicted by our model for two reasons. First, changes in length of the medial recti cause changes in the length of the lateral recti; the latter will cause recruitment/decruitment of abducens OMNs according to whether the muscle is stretched or shortened. Second, Keller and Robinson tested for vergence movements along the visual axis of one eye (as opposed to the midline); our model would predict that such movements would include both a conjugate and a vergence component, the former changing activity in the abducens. The neurophysiogiocal evidence is therefore consistent with our proposal that there is a signal (the vergence command) directed only at the medial recti.

If the vergence command were only directed at the medial recti, then one would expect differences in the kinematics of convergent and divergent eye movements. A number of behavioural studies have reported differences in the kinematics of convergent and divergent eye movements. Table 1 provides a summary of studies which have found ‘superior’ control dynamics in convergence. The essential feature of all these studies is that they are compatible with the notion of convergence occurring through active contraction of the medial recti, with divergence occurring via relaxation of the medial recti (with tension from the lateral recti causing the divergence). In summary, the available data are compatible with our idea that vergence commands are directed at the medial recti alone.

3.3 A relationship between the vergence and the conjugate command

According to the cyclopean EP model, a given conjugate command will need to take the current vergence command into account (and vice versa), if the desired gaze angle is to be achieved. A number of behavioural studies have supplied evidence for such interaction between the conjugate and vergence commands (e.g. Enright 1984, 1986; Judge and Cumming 1986; Miller et al. 1980; see Ono 1983 for a detailed discussion).

There is also neurophysiological evidence for a relationship between the vergence and conjugate commands. Mays and Porter (1984) have found that the majority of neurons in the primate abducens and oculomotor nuclei carry both conjugate and vergence signals. Similar results were reported by Keller and Robinson (1972) and Keeler (1973). On the other hand, Mays and Porter reported that the relative magnitudes of the conjugate and vergence signals were not closely matched for the neurons. Mays and Porter therefore suggested that conjugate and vergence signals are generated independently and combined for the first time at the motoneuron level. This arrangement is consistent with the behavioural evidence, which suggests that conjugate and vergence commands are not independent processes (Enright 1980, 1984; Erkelens et al. 1989a). The pooling of the signals at the motoneuron level results in a situation where one command has an influence on the other, but in which two separate systems generate the commands indepen-

Table 1. Evidence for differences in convergent and divergent eye movements (from Hung et al. 1997). The differences are all in favour of a higher performance during convergence when compared to divergence providing some support for our notion that vergence is directly driven via the medial, and not the lateral, recti

Differences	References
Peak velocity	Rashbass and Westheimer (1961)
Convergence > divergence	Miller (1973)
	Hung et al. (1997)
Initial phasic amplitude	Hung et al. (1997)
Convergence > divergence	
Response latency	Semmlow and Wetzel (1979)
Convergence < divergence	Hung et al. (1997)
Time to peak velocity	Rashbass and Westheimer (1961)
Convergence < divergence	Hung et al. (1997)
Time constant	Zuber and Stark (1968)
Convergence < divergence	Krishnan et al. (1977)
	Semmlow and Wetzel (1979)
	Hung et al. (1997)
Response duration	Hung et al. (1997)
Convergence < divergence	
Clinical observations	Borish (1970)
Relative vergence range	Ogle (1972)
Adaptability	Grisham (1983)
Heterophoria/fixation disparity curve	Daum (1986a, 1986b)
Convergence > Divergence	Ciuffreda (1992)

dently. Maxwell and King (1992) and Zee et al. (1992) have provided evidence in support of the idea that the conjugate and vergence systems are distinct at a neurophysiological level but that their actions interact. If the summing of the vergence and conjugate signals occurs at the motoneuron level as suggested, then a slight temporal asynchrony between the signals will produce a superposition of these movements. In fact, it is commonly observed that a 'pure' vergence movement has a small saccadic component (Erkelens et al. 1989a; Hering 1868/1977; Ono and Nakamizo 1978).

4 Observations on behaviour and perception

We will conclude by considering a number of experimental observations to demonstrate that the cyclopean EP model provides a useful framework for describing key features of the central commands responsible for controlling the oculomotor system.

4.1 Non-conjugate binocular adaptation

One advantage of the EP model is that it describes central ocular commands and hence uses language capable of distinguishing the changes in muscle force caused by central commands from those changes caused by a modification in the peripheral system. The cyclopean EP model suggests a mechanism for modifying binocular alignment: the commanded gaze angle is compared with the angle specified by afferent feedback and any discrepancies act as an error signal for the non-conjugate adaptation of eye movements. It has been well established that the eyes are capable of non-conjugate adaptation (e.g. Erkelens et al. 1989b; Lemij and Collewijn 1991; Schor et al. 1990) and such adaptation explains why Hering's law is so reliable over the developmental span.

In ideal circumstances, the eyes will move to the position dictated by the reciprocal conjugate command. Under such conditions there will be little or no afferent signal arising from the extra-ocular muscles when fixating at optical infinity as the extra-ocular muscles are subject to little or no load. The absence of any afferent feedback will signal zero torque, so that the afferent specified gaze angle will be at the origin of the coordinate system (and thus equal to R_c). A number of factors mean, however, that R_c will not suffice over a period of time. The relationship between the commanded and achieved gaze angle will be challenged for a variety of reasons, including developmental changes (in the eye and muscles), disease, trauma, fatigue, neuromuscular attrition or environmental factors such as refractive correction. It is clear that commanded gaze angle and ocular conjugacy will be compromised during life and that the binocular system requires a mechanism for calibration and adaptation. The cyclopean EP hypothesis suggests that afferent information would be required to signal error in any mechanism of calibration. The idea that afferent discharge is used in the long-term calibration of ocular position is not new; for example, Ludvigh (1952) proposed that afferent information provides long-term feedback for the maintenance of gaze position. We will later highlight a study (Lewis et al. 1994) that provides empirical support for this notion.

As we have already stated, under ideal conditions there will be no afferent discharge when the eyes are fixating objects at optical infinity. If ocular conjugacy is lost (e.g. due to an anisometropic spectacle correction), then one eye will make a smaller movement than required when binocular fixation is shifted. The sensory consequence of the lost conjugacy is horizontal retinal image disparity, which will stimulate the system to make a corrective vergence movement. In this situation, afferent feedback will arise because the muscles will be stretched beyond the threshold length specified by the conjugate system (note that this is true for any challenge to conjugacy, including damage to the medial and/or lateral recti and optical disruption). We propose that it is this afferent discharge that acts as an error signal, allowing the binocular system to recalibrate itself at a peripheral level. It should be noted that the vergence signal only acts as a reliable calibration signal in situations where there is no commanded vergence (i.e. when fixating at optical infinity). In circumstances where a vergence command is generated (i.e. when fixating proximal targets), the system is unable to distinguish between a fixation error due to the vergence system from one due to the conjugate system. It is therefore possible that afferent discharge only acts as an error signal when fixating objects with negligible vergence demand; it is thus interesting to note that non-conjugate adaptation occurs rapidly during distance fixation, but is largely absent when viewing near objects (van der Steen and Bruno 1995).

According to the cyclopean EP model, a degree of binocular alignment may even be maintained without visual feedback (although we assume that retinal image disparity provides the primary calibration signal). If retinal image disparity is removed (e.g. by covering one eye), then passive deviations of one eye relative to the other may still be sensed through afferent feedback (if a muscle is stretched beyond its threshold length). If afferent feedback is present, then it will act as an error signal regardless of whether it originated from retinal image disparity or not. Gauthier et al. (1994) carried out an experiment in which they covered one eye and then passively deviated this occluded eye. The passive deviation may be presumed to have created afferent feedback if we assume that the deviated eye's muscles were stretched beyond their threshold lengths. Gauthier et al. reported that the system did, indeed, adapt in a fashion designed to maintain ocular alignment. It is known, however, that prolonged patching of one eye will result in a loss of binocular alignment (Viirre et al. 1987). This suggests that over time the eyes drift in a manner undetected by the afferent transducers, so that visual information is essential for ocular conjugacy over long time periods. The preceding consideration suggests that afferent feedback is essential for the long-term maintenance of binocular alignment and conjugacy. In support of this idea, Lewis et al. (1994) have established that removal of ocular afferent feedback results in a loss of binocular alignment and conjugacy.

It will be seen that the afferent feedback required for non-conjugate adaptation generally relies on eye movements driven by retinal disparity, and thus retinal disparity plays an important role of calibration within the cyclopean EP model. This suggests that removing retinal image disparity will prevent non-conjugate adaptation (unless mechanical forces stretch a muscle beyond its threshold length). In line with this notion, Schor et al. (1990) have shown that disparity is necessary for the occurrence of non-conjugate adaptation. It should be noted, however, that retinal image disparity provides an error signal to two adaptive systems: (1) the conjugate system and (2) the vergence system. The vergence system contains a tonic element that adapts to reduce any steady-state demands placed upon the phasic response component. In contrast to the non-conjugate adaptive mechanism, the adaptable component of vergence does not require afferent feedback: the system relies purely on feedback from vision (viz. horizontal retinal disparity). This explains Lewis et al.'s (1994) finding that removal of afferent feedback caused a loss of binocular conjugacy whilst normal vergence adaptation was preserved. The presence of two systems which adapt to retinal image disparity also explains why non-conjugate adaptation occurs in two stages (Maxwell and Schor 1994). If ocular conjugacy is lost, then retinal image disparity will result and the system will attempt to overcome this disparity by making a vergence movement. In response to the vergence movement, adaptation of both the vergence and conjugate system will begin. Vergence adaptation is known to be rapid (e.g. Carter 1965; Schor 1979), whereas non-conjugate adaptation is relatively slow (e.g. Lemij and Collewijn 1991). The different time courses predict that a simple shift in vergence bias (heterophoria) will rapidly occur in response to a loss of conjugacy, with non-conjugate adaptation occurring at a later stage, exactly as reported by Maxwell and Schor (1994). Maxwell and Schor have pointed out that this arrangement allows the system rapidly to minimise disparity across the visual field before the higher level position-specific adaptation processes take place.

One key feature of the adaptive mechanism we propose is that the central command is compared with the sensed gaze angle to provide an error signal. This suggests that the system will selectively adapt the conjugacy of the eye movements according to the central command. It follows that adapting the saccadic system will not produce adaptation in the pursuit system, as these are separate control systems producing different central commands. In support of this, Schor et al. (1990) have reported that non-conjugate adaptation of pursuit does not transfer to the saccadic system and vice versa. On the other hand, it has been found that non-conjugate adaptation transfers between pursuit and gaze holding, suggesting that the central commands from these two systems have at least some similarity (Schor et al. 1990). One other feature of the cyclopean EP model is that it predicts that any non-conjugate adaptation can be specific to a particular gaze angle (as the system is controlling the equilibrium point of the movement). Such position specificity of adaptation has been demonstrated (Lemij and Collewijn 1992; Schor et al. 1993).

4.2 Spatial localisation

It is necessary for the nervous system to monitor ocular position in order that shifts in gaze direction do not lead to the perception of image displacement (whereas displacement of a target's image on the retina will lead to the perception of target movement during visual fixation). Helmholtz (1894/1924) provided one of the first proofs that efference copy plays an important role in the perception of visual direction by his observation that individuals with paralysis of an extraocular muscle perceive target motion when attempting to move their eye in the direction of the paralysed muscle. A number of other studies have confirmed the importance of efference copy for the perception of gaze direction (e.g. Brindley and Merton 1960; Stark and Bridgeman 1983). It has been reported, however, that attempts to move a completely paralysed eye do not result in target motion (Brindley et al. 1976; Stevens et al. 1976). These results provide support for the concept that both efference copy and afferent feedback are required for the perception of gaze direction.

According to the cyclopean EP model, both efference copy and afferent signals are required for the perception of visual direction and distance. This suggests that altering either the efference copy or afferent signal should modify the perception of visual direction and distance (the ocular equivalent to a ‘kinaesthetic illusion’). We are unaware of any studies that have directly explored whether modifying these signals changes the perception of egocentric distance (such studies would provide a critical test of the model). On the other hand, some indirect evidence supports the idea that afferent feedback is used in distance perception: Fiorentini et al. (1985a,b) demonstrated poor distance discrimination in cats following surgical deafferentation (by cutting the ophthalmic nerve) and Trotter and colleagues (Trotter et al. 1991, 1993) have shown that removing afferent feedback affects the mechanisms of distance perception.

In contrast to the limited studies on distance perception, a number of studies have explored the perception of visual direction following modification of either efference copy or afferent signals. If the cyclopean EP model is correct, altering efference copy will modify the central evaluation of the R_c and C_c commands. A perceived change in R_c will result in a change of the muscle characteristic which, in turn, will alter the interpretation of the afferent feedback (i.e. the origin of the coordinate system for monitoring afferent feedback will change). Likewise, a change in the C_c command will cause an incorrect scaling of the afferent signal and result in a modification of the perceived gaze angle. Conversely, if the afferent signals (A) are altered without a corresponding change in R_c and C_c, the perceived gaze angle will change. It may be seen that a change in R_c, C_c or A should alter the perceived gaze angle.

Some recent studies have modified the relationship between efference copy and afferent feedback to explore the effect of such a manipulation on the perception of gaze direction. Gauthier et al. (1990) artificially created a large heterophoria by deviating a covered eye using a suction lens. The results of this study provided evidence that ocular proprioception is used in the determination of target location, as the perceived visual direction was displaced in the same direction as the eye was deviated. Bridgeman and Stark (1991) modified both efference copy and afferent feedback to study their relative contributions to the perception of visual direction. The signals were modified by covering up one eye and then pressing a finger against either the viewing eye (altering efference copy) or the covered eye (altering afferent feedback). It was found that both of these manipulations caused a shift in perceived target direction. Bridgeman and Stark (1991) calculated the gain (across individuals) of the efference signal as 0.74 and the gain of the afferent signal as 0.13. Bridgeman and Stark’s estimate of the proprioceptive gain agrees well with the gain of 0.16 found by Gauthier et al. (1990). Lewis and Zee (1993) reported a higher gain (0.29) in their patient with trigeminal-oculomotor synkinesis. Lewis and Zee (1993) suggested that the lower gain found in the passive pointing experiments might be due to passive movement providing a relatively weak stimulus for the MTC receptors when compared to an active contraction (see Sodi et al. 1988). Whatever the reason for the differences in gain, all of these experiments may be interpreted in the following way: rotating the covered eye alters the afferent feedback without a corresponding change in R_c. Pressing against the viewing eye results in a change of the centrally evaluated R_c which, in turn, alters the interpretation of the afferent feedback. These experimental findings are therefore adequately described by the cyclopean EP model.

Steinbach and Smith (1981) demonstrated that spatial localisation can be reasonably accurate immediately following surgery for strabismus, despite the fact that the eye has been passively rotated. The only explanation for such a finding is that the nervous system is sensitive to afferent information. Steinbach and Smith’s conclusions have been challenged, however, by Bock and Kommerell (1986), who reported poor spatial localisation in their post-operative strabismic patients (the errors in localisation were predictable from the angle that the operated eye had been rotated through during surgery). Steinbach (1987) suggested that the differences in these two studies may be explained by the different anaesthetic techniques employed: Steinbach and Smith used general anaesthetic whilst Bock and Kommerell used a retrobulbar injection of local anaesthetic. It is likely that the retrobulbar injection caused a decrease in the total afferent activity (i.e. not just a selective decrease in the pain afferents). The decreased afferent activity would force the nervous system to rely on R_c alone when determining visual direction, and predictable post-operative errors would result. Furthermore, Bock and Kommerell reported that normal pointing accuracy was regained following several days of visual experience. It is possible that the return of normal pointing accuracy depended upon the dissipation of the anaesthetic and the return of the afferent signals.

4.3 The maintenance of binocular alignment and conjugacy

Evidence exists that the eye is capable of controlling eye movement in the absence of ocular proprioception (Guthrie et al. 1983). On the other hand, it is known that removing ocular proprioception leads to a long-term loss of saccadic conjugacy and ocular alignment (Lewis et al. 1994). These two findings are entirely consistent with the cyclopean EP model: the role of afferent inflow is to provide an error signal for *long term* adaptation and to supply information on egocentric distance during static conditions. The removal of ocular proprioception would therefore not be expected to have an immediate impact upon the control or perception of visual direction, but it would predict the long-term loss of binocular coupling. Visual information is necessary to ensure that the eyes maintain alignment (Viirre et al. 1987) but is not sufficient (Lewis et al. 1994). It has been suggested that dysfunction of ocular proprioception may play a role in the aetiology of strabismus (Corsi et al. 1990; Jurgens et al. 1981; Steinbach and Smith 1981). The cyclopean EP model is consistent with this view.

5 Conclusion

The cyclopean EP model provides a parsimonious and physiologically plausible account of oculomotor control and perception. A central feature of the model is the close relationship between the control and perception of ocular position. The framework serves a useful role in unifying a wide body of experimental findings, some of which have previously been perceived as conflicting. One major advantage of the framework is that it describes the control and perception of ocular position in a manner similar to current explanations for the control and perception of limb position. Furthermore, the model provides a hitherto lacking account of how ocular vergence can provide a perceptual signal for distance perception and suggests a fundamental role for the afferent discharge known to arise from the extraocular musculature. As the model is concerned with the central command processes, it distinguishes changes caused by central commands from those changes caused by peripheral adaptation. The model therefore serves a useful conceptual role when considering a number of recent studies on the non-conjugate adaptation of eye movements.

It should be emphasised in conclusion that the cyclopean EP model is speculative. It does, however, make a number of predictions which can be tested by quantitative modelling and biological experimentation. Whether or not subsequent investigations support the model, it gives a coherent starting point for the future exploration of the relationship between oculomotor control and perception.

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