Optimality of Position Commands to Horizontal Eye Muscles: A Test of the Minimum-Norm-Rule

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Dean, Paul, John Porrill, and Paul A. Warren. Optimality of position commands to horizontal eye muscles: a test of the minimum-norm rule. J. Neurophysiol. 81: 735–757, 1999. Six muscles control the position of the eye, which has three degrees of freedom. Daunicht proposed an optimization rule for solving this redundancy problem, whereby small changes in eye position are maintained by the minimum possible change in motor commands to the eye (the minimum-norm rule). The present study sought to test this proposal for the simplified one-dimensional case of small changes in conjugate eye position in the horizontal plane. Assuming such changes involve only the horizontal recti, Daunicht’s hypothesis predicts reciprocal innervation with the size of the change in command matched to the strength of the recipient muscle at every starting position of the eye. If the motor command to a muscle is interpreted as the summed firing rate of its oculomotor neuron (OMN) pool, the minimum-norm prediction can be tested by comparing OMN firing rates with forces in the horizontal recti. The comparison showed 1) for the OMN firing rates given by Van Gisbergen and Van Opstal and the muscle forces given by Robinson, there was good agreement between the minimum-norm prediction and experimental observation over about a ±30° range of eye positions. This fit was robust with respect to variations in muscle stiffness and in methods of calculating muscle innervation. 2) Other data sets gave different estimates for the range of eye-positions within which the minimum-norm prediction held. The main sources of variation appeared to be disagreement about the proportion of OMNs with very low firing-rate thresholds (i.e., less than ~35° in the off direction) and uncertainty about eye-muscle behavior for extreme (>30°) positions of the eye. 3) For all data sets, the range of eye positions over which the minimum-norm rule applied was determined by the pattern of motor-unit recruitment inferred for those data. It corresponded to the range of eye positions over which the size principle of recruitment was obeyed by both agonist and antagonist muscles. It is argued that the current best estimate of the oculomotor range over which minimum-norm control could be used for conjugate horizontal eye position is approximately ±30°. The uncertainty associated with this estimate would be reduced by obtaining unbiased samples of OMN firing rates. Minimum-norm control may result from reduction of the image movement produced by noise in OMN firing rates.

INTRODUCTION

Horizontal eye position1 is controlled principally by the actions of the two horizontal recti muscles, namely the medial and lateral rectus. Stable eye position is achieved when the forces exerted by these muscles balance the passive elastic force of the orbital tissues (which acts to restore the eye to near the primary position) so that there is no net torque on the eyeball. However, the requirement on the horizontal recti to counteract the passive torque only constrains the difference between the forces that are exerted by the two muscles not their individual magnitudes. This can be seen clearly in the case of the primary position itself: here the passive torque is essentially zero, so provided the force exerted by the medial rectus is equal to that of the lateral rectus, the eye will look straight ahead. For human eye muscles, the actual value of the force in the primary position is ~10 g (e.g., Carpenter 1988). How has the oculomotor control system arrived at this value?

Answering this question is necessary for understanding the principles underlying the control of eye position, and as such is relevant both to normal function and to those clinical conditions in which the control of eye position is not normal. Also the selection of force magnitudes in the extraocular muscles (EOMs) is an example of a fundamental and widespread control problem that arises whenever there are more muscles acting on a joint than there are degrees of freedom through which the joint can move. It is possible that the strategy used by the oculomotor system to solve this redundancy problem may have general application.

A quantitative solution to the redundancy problem for EOMs has been proposed by Daunicht (1988, 1991). Daunicht considered the task faced by the control system in maintaining the eye a small distance from its current position, for example the primary position. Increasing the command signals to both horizontal recti, thereby producing cocontraction, would not be efficient for this purpose: in the worst case, the change in motor commands would produce no change in position at all. In contrast, the most efficient change in motor commands is the one that gives the maximum change in eye position. Daunicht proposed that the oculomotor system uses the most efficient changes in motor command, which in effect means that any particular change in eye position is maintained by the smallest possible change in motor commands. “Smallest possible” here refers to the smallest possible sum of the squared changes in motor commands (see METHODS): if the changes in motor command are considered to form a vector, this corresponds to the minimum norm or magnitude of the vector. “Minimum norm” control is therefore the term used in the present study for the proposed control principle, in preference to the possibly confusing term “minimum effort” (Daunicht 1988).

Daunicht’s scheme is, to our knowledge, the most developed quantitative solution so far suggested for the redundancy problem in extraocular motor commands. Moreover, its underlying principle (sometimes referred to as pseudoinverse control) has...
been proposed as a general method for both biological and artificial motor systems (e.g., Klein and Huang 1983; Pellionisz 1984). The present study therefore sought to determine whether Daunicht’s scheme is in fact consistent with published data on the behavior of EOMs and ocular motoneurons (OMNs). The study’s scope is restricted to consideration of horizontal eye position despite the fact that Daunicht’s proposal deals with three-dimensional eye position, because even in the simplified case relating the minimum-norm rule to experimental data are far from straightforward. For the same reason, this study deals only with the motor commands that relate to conjugate eye position.

For horizontal eye position, the minimum-norm principle predicts that a small change in position will be associated with an increase in the motor command to the agonist muscle and a decrease in the command to the antagonist muscle and that the magnitude of the changes in command will be directly proportional to the strength of the muscle in each case. The first of these is a qualitative prediction, long known as reciprocal innervation and possibly attributable to Descartes (Sherrington 1947). It is the second, quantitative, prediction that is the distinctive contribution of the minimum-norm principle and one that requires operational definitions of the terms motor command and muscle strength.

The original definition of change in motor command was ‘‘motor activity change’’ (Daunicht 1988). An obvious referent for this phrase would be the change in summed activity of the efferent nerves to a given muscle, corresponding to the change in summed activity of the parent pool of OMNs. The firing rates of OMNs in relation to eye position have been obtained by electrophysiological recording in awake monkeys (Fuchs et al. 1988; Gamlin and Mays 1992; Keller 1981; King et al. 1981; Van Gisbergen and Van Opstal 1989). A striking feature of OMN pool activity, not explicitly mentioned by Daunicht, is the way it increases nonlinearly when the eye moves into the ON direction of the relevant muscle as individual OMNs and their associated motor units are recruited. Because of recruitment, the change in motor command (as interpreted here) that corresponds to a fixed small change in eye position varies very markedly over the ocularmotor range.

The original definition of muscle strength was as a ‘‘coefficient . . . of . . . neuromuscular transmission’’ (Daunicht 1991), which could be derived from the slope of the relation between muscle tension and neural activity (Daunicht 1988). Given the preceding interpretation of motor command, the strength of an EOM at a given eye position corresponds to the isometric change in muscle force produced by a unit change in summed activity of the OMN pool at that position. A crucial feature of muscle strength defined in this way is that its magnitude is determined by the manner in which motor units are recruited (as described in detail in METHODS). For example, if motor units are recruited in order of increasing strength (the size principle), then the ‘‘muscle strength’’ of an EOM also will increase as the eye moves to positions further in the EOM’s direction of action.

One consequence of the dependence of muscle strength on recruitment is that the minimum-norm principle is in fact making precise predictions about motor-unit recruitment in EOMs. A second consequence is that direct measurements of EOM muscle strength as a function of eye position are not available (see METHODS). However, the values of isometric-force gradient needed for the estimation of muscle strength can be derived from measurements of extraocular muscle tension as a function of muscle length and fixation command in people (e.g., Miller and Demer 1994; Miller and Robinson 1984; Robinson 1975; Simonsz and Spekreise 1996), on the assumption that monkey and human do not differ significantly with regard to OMN activity or extraocular muscle properties. The present study obtains estimates for the range of horizontal eye positions over which the minimum-norm rule holds by using the muscle-force measurements in combination with Daunicht’s proposal to generate predicted changes in motor commands. These then are compared with the actual changes observed electrophysiologically. Preliminary findings have been published previously in abstract form (Dean et al. 1996).

It should be emphasized that, although Daunicht’s minimum-norm rule relates changes in motor command to changes in position, it is not concerned with the movements by which those changes are achieved. Minimum-norm control deals only with commands to the eye muscles when the eye is in static equilibrium. Movement commands, especially those for fast saccadic movements, may be far from minimum norm. One advantage of restricting the problem in this way is that complex issues of plant dynamics can be ignored.

METHODS

This section is divided into five parts. The first describes the basic relationships among muscle force, length and fixation command in EOM. The second indicates how Daunicht’s minimum-norm rule can be derived for the one-dimensional case. The third and fourth sections consider how the two key terms, motor command and muscle strength, in the derivation should be interpreted in the light of the data on the recruitment of motor units in the EOMs. Finally, methods for estimating isometric-force gradients are outlined.

Length-tension relationships for EOM

The static force exerted by an EOM is a function of both its length and the fixation command signal delivered by its parent nerve. One method for measuring this function in the human lateral rectus muscle (Robinson et al. 1969) is shown schematically in Fig. 1A.

The lateral and medial recti from one eye (shown in Fig. 1A as the left eye) are detached in preparation for strabismus surgery. The lateral rectus is attached to a strain gauge, enabling its length (L) to be fixed and its tension (T) to be measured while the subject fixates a target at location Ψ with the right eye. Assuming Hering’s law of equal innervation by which the same fixation command also is passed to the left eye, it is possible to plot T as a function of L at different values of fixation command Ψ (Fig. 1B). In this figure, the length of the left lateral rectus L is transformed into an equivalent eye position Ψdeg.

The sign convention adopted in Fig. 1B is that left is positive, i.e., stretching the left lateral rectus corresponds to a decrease in Ψdeg. The behavior shown in Fig. 1B can be described by a family of hyperbolic curves as suggested by Robinson (1975). The version of Robinson’s equation used here is

\[ T = \frac{k}{2}(\phi + c) + \frac{k^2}{4}(\phi + c)^2 + a^2 \]
displacements produced by different levels of innervation to the left lateral rectus as specified by the fixation commands corresponding to target shorter than the primary-position length, i.e., the eyeball rotated left in the pulling direction of the muscle. Five curves shown are by 

Initially at the surface of the globe, then this balance can be represented acting on it must balance out. If the forces concerned all act tangent-

The relation between tension $T$ and muscle length $\phi$ depends on the three parameters $k$, $a$, and $e$. The hyperbolic shape of the length-tension curves reflects the observations that when an EOM is stretched far enough (Fig. 1B, left) at a given level of fixation command, it behaves like a spring with constant elasticity, i.e., tension proportional to length (parameter $k$). When the muscle is unstrained, its tension is zero. The transition between the two states is gradual rather than abrupt, as indicated by the curvature parameter $a$ (deg). Changing the fixation command to the muscle preserves the overall pattern of response but alters the point at which the transition to “stretched” behavior occurs. The “innervation” parameter $e$ (deg) corresponds to the amount the basic curve is shifted along the $x$ axis as the fixation command $\phi$ changes. Determination of the relationship between $e$ and $\phi$ is described later (Estimation of isometric force gradients).

Minimum-norm rule for horizontal eye position

Daunicht’s derivation of the minimum-norm rule for all six EOMs (Daunicht 1988, 1991) is simplified here to the case of the two horizontal recti controlling horizontal eye position. (Steps to assess the effects of this simplification and of Daunicht’s own simplifications concerning the mechanical details of the EOM system are described in the final part METHODS). Figure 2A shows the eye at equilibrium, looking $\phi$ deg to the left. Because the eye is not moving, the torques acting on it must balance out. If the forces concerned all act tangential at the surface of the globe, then this balance can be represented by Eq. 2

$$f_1 - f_2 = F_{OT}$$

where $f_1$ is the force exerted by the agonist muscle, $f_2$ is the force exerted by the antagonist muscle, and $F_{OT}$ is the force exerted by the stretched orbital tissues (forces pulling to the left are positive). $F_{OT}$ is a possibly nonlinear function of eye position: the $f$s are the nonlinear functions of muscle length and fixation command sent to the muscle described by Eq. 1.

Daunicht (1991) made use of the fact that for a very small displacement of the eye from equilibrium (Fig. 2B), the system behaves linearly (see APPENDIX: Derivation of minimum-norm rule for horizontal eye position). It is therefore possible to calculate the change in eye position $\delta \phi$ produced by two (small) arbitrary changes in motor command to the two muscles, $\delta m_1$ and $\delta m_2$ (Eq. 3: derived as Eq. A6 in the APPENDIX)

$$z_1 \delta m_1 - z_2 \delta m_2 = (\xi_1 + \xi_2 + L) \delta \phi$$

where

$$z_1 = \frac{\partial f_1}{\partial m_1} (m_1, \phi)$$

$$z_2 = \frac{\partial f_2}{\partial m_2} (m_2, \phi)$$

In this equation, $L$ is the coefficient of elasticity of the orbital tissues measured at the eye position $\phi$, and $\xi_1$ and $\xi_2$ are the coefficients of elasticity of the two muscles measured at eye position $\phi$ and baseline levels of motor command $m_1$ and $m_2$, respectively. The terms $z_1$ and $z_2$ represent the muscle strengths, which correspond to the isometric force gradients also measured at eye position $\phi$ and baseline levels of motor command $m_1$ and $m_2$ respectively (see APPENDIX).

Equation 3 is a precise representation of the redundancy problem for horizontal eye position, showing not only that a given small change in position can be brought about by (infinitely) many combinations of change in motor command but also giving the actual change.
in eye position that any given combination will produce. Two particular sets of combination are relevant to the present study. The first is the set that produces no change in eye position. Setting $\delta \phi$ to 0 in Eq. 3 gives Eq. 4.

$$z_i \delta m_1 = z_2 \delta m_2$$  \hspace{1cm} (4)

The equation is represented diagrammatically in Fig. 3A, which plots one motor command against the other and draws a line through those points that produce the particular eye position $\phi$ if the values of the $z$s do not change (cf. Feldman 1981). The gradient of this “iso-position” line is $z_i/z_2$. This implies that for keeping the eye in one place, the commands to the two eye muscles must be increased (or decreased) and that the change in command to the weaker muscle must be larger than that to the stronger muscle to maintain the balance.

The second important set of motor-command changes is illustrated in Fig. 3B, which shows the iso-position line from Fig. 3A (labeled $\phi$) together with a very close iso-position line labeled $\phi + \delta \phi$. Here the change in motor commands has been chosen to give a point on the new iso-position line such that the line segment that joins points $(m_1, m_2)$ and $(m_1 + \delta m_1, m_2 + \delta m_2)$ is at right angles to the original iso-position line. Two consequences follow from this choice. The first is that because of the right angle, the gradient of the line segment can be deduced from the gradient of the original iso-position line shown in Eq. 3. It is

$$\frac{\delta m_1}{\delta m_2} = \frac{z_1}{z_2}$$  \hspace{1cm} (5)

The second consequence is the line segment represents the shortest distance between the point $(m_1, m_2)$ and the new iso-position line. The set of motor command changes $(\delta m_1, \delta m_2)$ are therefore the smallest possible that will produce $\delta \phi$ (see APPENDIX for formal derivation) or in other words they are the minimum-norm changes in command. In contrast to the changes in motor commands that maintain position, the most effective changes in commands for producing change in position are of opposite sign to the two muscles (reciprocal innervation), with the stronger muscle getting the bigger change. A more general method used by Daunicht to derive minimum-norm commands for eye position in three dimensions is outlined in the APPENDIX (Pseudo-inverse control).

**Interpretation and measurement of $\delta m$**

To test whether the prediction of Eq. 5 is borne out experimentally, the terms of the equation have to be defined operationally. The original definition of $\delta m$ was as a “motor activity change” (Daunicht 1988). As indicated in INTRODUCTION, an obvious interpretation of this phrase would be the change in activity of neurons within the relevant pool of OMNs, as illustrated for the schematic distributed model of Fig. 4 (cf. Dean 1996). In response to a change in fixation command $\delta \phi$, the firing rate of the 7th OMN in a pool of $n$ OMNs changes by $\delta(FR_i)$. The sum of these changes in firing rate would then correspond to

$$\delta m = \sum_{i=0}^{n} \delta(FR_i)$$  \hspace{1cm} (6)

A problem with this definition is that the changes in firing rates are produced by a change in fixation command $\delta \phi$, the nature of which is not directly known. However, provided the oculomotor system is functioning normally, for conjugate eye positions there is a fixed relationship among $\phi$, the central fixation command to any one of the six OMN pools, and three of its effects: eye position $\phi$, OMN firing rates, and force in the corresponding extraocular muscle. This means that there is also a fixed relationship between any two effects of $\phi$, in this instance OMN firing rates and eye position $\phi$. The relation of OMN firing rate to eye position is

$$FR = K(\phi - \theta) \text{ for } \phi > \theta$$

$$= 0 \text{ otherwise}$$  \hspace{1cm} (7)

which indicates that firing rate varies linearly with eye position above the OMN’s threshold position $\theta$ e.g. (Keller 1981). $K$ represents the
A fundamental feature of OMN pools is that the threshold \( \theta \) varies between OMNs, so that as the eye moves into the ON direction of the muscle controlled by the pool, the number of active units increases. In other words, a basic feature of the fixation command \( \psi \) is that it can recruit OMNs as it gets stronger. The change in motor command \( \delta m \) corresponding to a fixed change in position \( \delta\psi \) necessarily increases as \( \psi \) increases

\[
\delta m = \sum_{j=0}^{i} \delta(FR_j) = \sum_{j=0}^{i} K_j \delta\psi 
\]

where \( j \) units have been recruited

This quantity can be conveniently measured using the gradient of the summed firing rates of the OMN pool when plotted against eye position

\[
\delta m = \frac{d(\sum \text{FR}_i)}{d\psi} \delta\psi
\]

A number of data sets is available for the firing rates of OMN pools. The initial set used in the present study was that shown in Fig. 1 of the review by Van Gisbergen and Van Opstal (1989). This figure plots the slope \( K \) against threshold \( \theta \) for 87 OMNs, the firing rate characteristics of which were measured in four previous studies. One of these (Robinson 1970) was of the primate oculomotor nucleus, the remaining three (Fuchs and Luschei 1970; Goldstein 1983; Skavenski and Robinson 1973) were of the primate abducens nucleus. All the studies found that the OMN firing slopes \( K_i \) increased as \( \theta_i \) increased, that is, as recruitment proceeded. The graph points were converted with Flexitrace software to numerical data, which then were used to calculate the gradient of total OMN firing rate with respect to position, corresponding to the measurement of \( \delta m/\delta\psi \). A few of these units, so the relationship

1) The thresholds for 160 OMNs are shown in a histogram in Fig. 2C of a review by Keller (1981). These are taken from four experiments, two of which (Fuchs and Luschei 1970; Robinson 1970) also contributed data to the set of Van Gisbergen and Van Opstal (1989) described earlier. The two additional studies were by Schiller (1970) on OMNs in the oculomotor and abducens nuclei and by Keller and Robinson (1971) on the abducens nucleus. The review does not give explicit values for the slope \( K \) of these units, so the relationship between \( K \) and threshold \( \theta \) estimated by Van Gisbergen and Van Opstal (1989) was used to estimate \( K \). An additional estimate was made of the thresholds of the units lumped in the histogram bin labeled ‘‘45 (deg) off,’’ on the assumption derived from the remainder of the data that the number of units per 5° bin decreased linearly as the threshold increased.

2) Slope is plotted against threshold for 78 OMNs in Fig. 2A and B, of the study by King et al. (1981). The units were recorded from the oculomotor and trochlear nuclei.

3) Slope is plotted against threshold for 81 OMNs in Fig. 5 of the study by Fuchs et al. (1988). These were recorded in the abducens nucleus, and were identified as motoneurons by spike-triggered averaging of the lateral rectus electromyographic (EMG).
The threshold and slope (for conjugate eye positions) is given for 74 medial rectus motoneurons in Table 1 of Gamlin and Mays (1992). As with other OMNs, these units showed a positive correlation between firing-rate slope $K_i$ (for conjugate eye positions) and threshold $u_i$.

Interpretation and measurement of $z$

The original interpretation of $z$ was as a “coefficient . . . of . . . neuromuscular transmission” (Daunicht 1991), which could be derived from the slope of the relation between tension and neural activity (Daunicht 1988). This interpretation does not deal explicitly with the problem of recruitment of motor units. Figure 4 illustrates how a change in fixation command $d\phi$ produces a change in muscle force in a distributed model of the OMN pool and its associated motor units. The change in fixation command alters the firing rates of the recruited OMNs in the pool $[\delta(FR_1) \ldots \delta(FR_j)]$ (Eq. 9). The altered firing rates in turn change the forces delivered by the motor units $(\delta f_1 \ldots \delta f_j)$, which in the simplified system of Fig. 4 are assumed to sum to the change in total muscle force $\delta f$ (for further details, see Dean 1996; for qualifications, see Goldberg and Shall 1997; Goldberg et al. 1997a). In normal operation, the change in motor command produces a change in eye position, so that $\delta f$ depends on both the change in fixation command and the change in position (Eq. 1: Eq. A3). The change due to fixation command alone is the change in isometric force, here termed $\delta F_i$. The distributed model therefore gives rise to the following expression

$$z = \frac{\delta F}{\delta m} = \left(\frac{\sum_{r=1}^{n} \delta F_i}{\sum_{r=1}^{n} \delta (FR_i)}\right)$$

where $j$ motor units have been recruited, and $\delta F_i$ is the change in isometric force generated in the $i$th unit by the change $\delta (FR_i)$ of its parent OMN.

Measurements in cat indicate that for recruited units the isometric change in force is approximately linearly related to the change in stimulation frequency (e.g., Shall and Goldberg 1992)

$$\delta F_i = y_i \delta (FR_i)$$

where $y_i$ can be regarded as a measure of the strength of the motor unit (cf. Dean 1996). Assuming simple summation of the changes in force generated by individual motor units, then the change in force for the whole muscle is given by Eq. 13.

$$\delta F = \sum_{r=1}^{n} \delta F_i = \sum_{r=1}^{n} y_i \delta (FR_i) = \sum_{r=1}^{n} y_i K_i \delta \phi$$

Therefore

$$z = \frac{\delta F}{\sum_{r=1}^{n} K_i}$$

Equation 14 indicates that $z$ is not an easy quantity to measure directly because it is not simply an intrinsic property of the muscle. It depends on the manner in which the fixation command recruits motor units. This would not be a problem if all motor units were of equal strength because $z$ then would be a constant. However, it is known that EOM motor units are not of equal strength (for review, see Goldberg 1990). If (for example) $y_i$ was to increase with recruitment, then so would $z$. Moreover, for any recruitment order, the influence on $z$ of units recruited later is greater than those recruited earlier because $z$ is a gradient measure and the OMN firing slopes $K_i$ increase as recruit-
ment proceeds (see preceding text). It is not therefore possible to measure \( z \) directly in primate EOM by using electrical stimulation of the parent nerve.

Fortunately, it is possible to bypass \( z \) when testing the prediction of the minimum-norm rule given in Eq. 5. A change in fixation command \( \delta \phi \) gives rise to three effects: a change in OMN firing rates \( \delta m \), a change in muscle force \( \delta f \), and a change in eye position \( \delta \phi \). As mentioned above, in the normally functioning eye, the relation between these three effects is fixed. Thus the isometric component \( \delta f \) of the change in individual muscle force can be related to change in firing rates, as in Eq. 11.

\[
\delta F = z \delta m
\]

It follows that

\[
\frac{\delta F_1}{\delta F_2} = \frac{z_1 \delta m_1}{z_2 \delta m_2}
\]

where the subscripts 1 and 2 refer to the two horizontal recti. But Eq. 5 shows that if the minimum-norm rule is obeyed, the ratio of the \( z \)s is the same as that of the \( \delta m \)s. Thus

\[
\frac{z_1 \delta m_1}{z_2 \delta m_2} = \frac{\delta m_1^2}{\delta m_2^2}
\]

so that

\[
\frac{\delta F_1}{\delta F_2} = \frac{\delta m_1^2}{\delta m_2^2} \tag{15}
\]

Because \( \delta m \) has been defined operationally in terms of firing-rate gradient for the oculomotor pool (Eq. 10), Eq. 15 formulates the prediction from the minimum-norm rule in terms of measurable quantities. The terms on the left-hand side derive from measurements of the length-tension curves in whole EOMs: the terms on the right-hand side derive from measurements of the firing rates of individual OMNs. The relationship between the two embodied in Eq. 15 is thus fundamental for testing the prediction of the minimum-norm rule.

Although the values of \( z \) are bypassed for the purpose of testing the minimum-norm prediction, they are important for interpreting the outcome of the test in terms of motor-unit recruitment (see INTRODUCTION). The values therefore are derived (as \( \delta F/\delta m \)) in a subsequent section of RESULTS.

**Estimation of isometric force gradients**

As indicated in Fig. 4, the fixation command \( \delta \phi \) produces a change in eye position \( \delta \phi \) in the normally functioning eye. Both \( \delta \phi \) itself, and the change in muscle length produced by \( \delta \phi \), alter the force exerted by the muscle (\( \delta f \)). If, however, the length of the muscle is fixed, then the change in muscle force (\( \delta F \)) is caused only by the change in motor command. The quantity \( \delta F \) can be estimated from the isometric-force gradient, measured with respect to fixation command (referred to hereafter simply as isometric-force gradient). The behavior of EOMs described by Eq. 1 allows this isometric-force gradient to be calculated (either analytically or numerically) for values of eye position and fixation command interpolated between those at which the original measurements were taken. As with the measurements of \( \delta m \) (see preceding text), the present study used an initial set of values for the parameters in Eq. 1, then subsequently explored the effects of varying those parameters on the minimum-norm prediction.

The initial parameter values were derived from the model described in Robinson (1975), as follows.

The parameter \( k \) in Eq. 1 corresponds to the coefficient of elasticity of the stretched muscle with respect to change in eye position. Robinson (1975) gives these coefficients with respect to percentage change in muscle length. They are converted here to the coefficients for change in eye position, using the values for muscle length given in Robinson (1975) and assuming that a 1° change in eye position corresponds to a 0.2074 mm change in muscle length. The values are 0.76 g/mm for the lateral rectus and 1.01 g/mm for the medial rectus.

The parameter \( a \) determines how curved the transition is between the two straight line portions of the curve in Eq. 1. Its dimensions are those of force, and the value given in Robinson (1975) is 6.24 g for lateral rectus and 6.49 g for medial rectus.

The parameter \( e \) corresponds to the amount the basic curve in Eq. 1 is shifted along the \( s \) axis as the fixation command changes. It can be derived from the kind of data shown in Fig. 1B, and values so obtained are shown in Fig. 3 of Robinson (1975). These were from the horizontal recti of strabismic patients (Collins 1971; Collins et al. 1969; Robinson et al. 1969), described as an “average of all results to date provided by C. C. Collins and D. M. O’Meara” (Robinson 1975). However, these values (termed “primary innervation” by Robinson) require adjustment if the net muscle force of an agonist-antagonist pair is to equal the force exerted by the orbital tissues. This adjustment is termed “secondary innervation,” and its derivation given in the APPENDIX (Secondary innervation and the parameter \( e \)). The best fit quartic curves to the resultant values of \( e_1 \) (for lateral rectus) and \( e_2 \) (medial rectus) are given in Eq. 16.

\[
e_1 = 4.42 + 0.6356 + 0.0127^2 + 3.84 \times 10^{-3} \psi^2 - 8.27 \times 10^{-3} \psi^4
\]

\[
e_2 = 4.17 - 0.6267 + 0.0127^2 - 3.40 \times 10^{-3} \psi^2 - 8.73 \times 10^{-3} \psi^4
\]

and are illustrated in the APPENDIX (Fig. A1). Following the usage in Robinson (1975), the parameter \( e \) is expressed as percentage change in muscle length rather than as the equivalent change in eye position.

The length-tension curves for the lateral rectus muscle using these values of \( e_1 \) with secondary innervation are shown in Fig. 5A (---). In addition to the experimentally obtained curves (cf. Fig. 1), Fig. 5A shows the “natural” length-tension curve (---), which indicates the forces obtained when the muscle is at the length prescribed by the fixation command. A similar natural curve can be calculated for the medial rectus muscle (Fig. 5B): the difference between the two, adjusted for sign, closely matches the experimentally observed values for orbital force (APPENDIX: Eq. A16). This demonstrates that the method for deriving \( e_1 \) and \( e_2 \) was successful and that the resultant model is consistent. Finally, the isometric-force gradient with respect to fixation command, \( \delta F/\delta \phi \), can be calculated for each muscle from Eqs. 1 and 16, as described in the APPENDIX (Isometric force gradient with respect to fixation command).

Subsequently, the values of the three parameters in this basic model were varied to test the robustness of the minimum-norm prediction.

**PARAMETER \( k \).** Two main alterations have been proposed to the original model for this parameter. One is that the medial and horizontal recti are of similar stiffness (and length), as argued by Clement (1987) and Simonsz and Spekreijse (1996). The second is that the original values for the stiffness were too high (Miller and Robinson 1984; Simonsz and Spekreijse 1996). Isometric force gradients as a function of eye position therefore were calculated for two identical muscles and for half the original stiffness.

**PARAMETER \( a \).** Relatively little attention has been paid to this parameter, possibly because the EOMs normally operate in regions of the length-tension curve that are approximately linear (Fig. 5A). Here, isometric-force gradients were calculated for values of \( a \) half or double the original values.

**PARAMETER \( e \).** As described in the preceding text, one feature of the original model was its use of secondary innervation. The effects of this were examined by calculating isometric-force gradients for the original estimates of the parameter \( e \), that is primary innervation (see APPENDIX, Eq. A14). Also, Clement (1985) has suggested slightly different values of \( h \) and \( w \) for the equation for secondary innervation (APPENDIX, Eq. A17). Isometric force gradients were therefore calculated for Clement’s values, namely \( h = 5.5, w = 9.0 \).
In addition to these variations in a single parameter, three more complex variants of the original model were investigated.

1) The full three-dimensional EOM model of Miller and Robinson (1984) was implemented and adjusted so that its performance resembled that of ORBIT (Miller and Shamaeva 1995). The isometric-force gradients of the model to changes in horizontal fixation command then differed from those derived from the earlier set of measurements in lacking cubic or higher terms, i.e., it is a simple quadratic function. It also differs in that the orbital force resulting when two symmetrical muscles using this equation are opposed is not zero, but a linear function of eye position with slope 0.4 g/°. Thus secondary innervation is not required to balance the orbital force. Isometric force gradients were calculated for these parameter values.

2) All the variants considered so far are derived from the same original set of measurements, of length-tension curves in detached horizontal recti (see preceding text). A new set of measurements was obtained by Collins and coworkers (Collins et al. 1975) on four strabismus patients, using force transducers implanted in series between the tendon of a muscle and its severed insertion in the globe. Each transducer was calibrated by attaching a suture between the tendon of a muscle and its severed insertion in the globe. Force transducers implanted in series between the tendon of a muscle and its severed insertion in the globe. Each transducer was calibrated by attaching a suture between the tendon of a muscle and its severed insertion in the globe.

Each transducer was calibrated by attaching a suture between the tendon of a muscle and its severed insertion in the globe. Each transducer was calibrated by attaching a suture between the tendon of a muscle and its severed insertion in the globe.

3) Simonsz and Spekreize (1996) describe a version of the original Robinson model simplified for easy clinical use. It employs symmetrical horizontal rectus muscles and lower values of stiffness, as described in the preceding text. In addition, the tension in passive muscle (i.e., with no innervation) increases exponentially with length when the muscle is stretched rather than linearly as in the original model. The basis for this exponential increase is a series of measurements (Simonsz 1994; Simonsz et al. 1986, 1988) on detached horizontal recti in strabismic patients under either general (n = 80) or local anesthetic (n = 32). However, the length-tension curve was linear for contracting muscle, whether the contraction was produced voluntarily (Simonsz 1994) or by injection of succinylcholine (Simonsz et al. 1988). This difference between innervated and passive muscle means that the length-tension curves are compressed along the tension axis (e.g., Fig. 14A), with consequent alteration of the isometric-force gradients. The precise effects of the compression cannot be directly explored with the model of Simonsz and Spekreize (1996), because in that model innervation is taken to be zero for a fixation command of ~30°. It was thought important to explore them, however, because they appeared likely to improve the fit of the minimum-norm prediction for large deviations of the eye (more than ~30°). An indirect method therefore was chosen that consisted of asking what the length-tension curves of the horizontal recti would look like if the

\[
e = 13.169 + 1.249\psi + 0.01\psi^2
\]
minimum-norm rule were obeyed exactly. Details of this procedure are given in the Appendix (Minimum-norm equations for muscle).

RESULTS

If the horizontal eye-position control system were using the minimum-norm rule as described by Daunicht (1988, 1991), then there would be a particular relationship between the strengths of the horizontal recti muscles and the motor commands sent to them to produce a small change in the position of the eye. The command to the agonist muscle should increase and that to the antagonist muscle decrease (reciprocal innervation); and the size of the change should be proportional to the strength of the muscle (METHODS, Eq. 5).

The motor command to a muscle is interpreted here as meaning the summed firing rates of the parent OMNs, and so the strength of the muscle is measured as the change in isometric force produced by unit change in summed firing rate. Because muscle strength so defined is crucially dependent on recruitment strategy and therefore difficult to measure directly, a more convenient way of testing the minimum-norm rule is to use the equivalent relationship depicted by Eq. 15 of METHODS. This relationship links two quantities: the ratio of the firing-rate gradients of the two OMN pools and the ratio of the isometric-force gradients of the two muscles. The minimum-norm rule predicts that the latter equals the square of the former.

Testing this prediction therefore requires comparison of data for OMN firing rates with data for EOM isometric-force gradients. The comparison is carried out as follows. First, the basic data sets described in METHODS are compared. Second, the effects on this comparison are assessed for variations in each data set in turn. Finally, the data are used to derive an indirect measurement of muscle strength so that the relation between motor unit recruitment and the minimum-norm rule can be demonstrated.

Comparison of basic data sets

The basic data set for the firing rates of OMNs was taken from the review of Van Gisbergen and Van Opstal (1989). The summed firing rates of the OMNs in that data set are shown as a function of fixation command (and hence eye position—see METHODS) in Fig. 6A. Recruitment begins at about −60° and stops at about +25°. This is easier to see in the plot of the gradient of summed firing rate that is shown in Fig. 6B. The gradient changes slowly below approximately −40°, then increases almost linearly until it levels out fairly abruptly about +25°. It is this gradient that is taken here as corresponding to the small change in motor command δm that produces a small change in eye position δφ (e.g., Fig. 3). The method of testing the minimum-norm rule described in METHODS requires the ratio of δm1 and δm2 for the two horizontal recti. The initial assumption here is that the OMN pools for the two muscles behave identically with respect to their own ON directions so that the firing-rate gradient shown for one of the OMN pools in Fig. 6B can be reflected simply around the line representing the primary position (ψ = 0) for the other muscle. The ratio of these two gradients is plotted on a logarithmic scale in Fig. 6C. The plot is approximately linear in the range −30 to +30°, which means that the logarithm of the ratio changes by equal amounts for equal changes in eye position. Outside this range, the firing-rate gradient of the off-direction muscle starts to decline more rapidly: the ratio of the gradients therefore increases (more than +30°) or decreases (less than −30°) more sharply than it does within the 30° range. Overall, the ratio of the two gradients, representing the ratio of the changes in motor commands on the left hand side of Eq. 15, varies by >100-fold over the oculomotor range.

The basic data set for isometric-force gradient is taken from the model described in Robinson (1975), and the gradients for lateral and medial recti plotted as functions of eye position in
predicted values, and the squaring is introduced so that positive and negative errors do not cancel. In this case, the values are of ratios, so the difference between the logarithms of the observed and predicted values becomes the appropriate measure, thus avoiding the relative underweighting of errors for low expected values. The plot, in Fig. 8B, which omits the error score of 0 at the primary position, shows clearly how the error increases sharply outside the range ±30°. The sum of the squared errors (for 5° steps) within this range was 0.156 in contrast to the value of 5.92 for the range ±30–45°.

The method for deriving the fit shown in Fig. 8 is in some respects less intuitive than thinking of the minimum-norm rule in terms of iso-position lines, as described in the introduction. The purpose of Fig. 9 is to illustrate the equivalence of the two approaches by showing that the data underlying Fig. 8 also produce the appropriate pattern when plotted with relation to iso-position lines. This graph plots the iso-position curves at 10° intervals from −40 to +40°. The muscle model used is a slight variant of that derived from Robinson (1975) in which the horizontal recti are equal (see Methods). It can be seen that the line connecting the actual firing-rate commands crosses the iso-position lines at ~90° within the ±30° range of eye positions (cf. Fig. 5B), but outside this range crosses the −40 and +40° iso-position lines at an angle >90°. Thus this representation also shows that the data are consistent with the minimum-norm prediction only within about ±30°.

One advantage of iso-position line diagrams is that they show clearly the effects of different representations of motor command. Thus Fig. 10A shows what happens when the motor commands are not summed firing rates but are linearly related to eye position φ. It can be seen from Fig. 10A that even if some level of the oculomotor system uses such commands, it does not minimize the norm of their changes.

Similarly, Fig. 10B plots the iso-position lines in terms of the innervation parameters $e_1$ and $e_2$ of the two muscles. The natural operating region of an EOM (Fig. 5A) is in those parts of the length-tension curves where the slope (i.e., stiffness) is approximately constant. In this region, the isometric-force gradient at a given position of the eye is the product of the muscle’s (fixed) stiffness and the gradient of its innervation parameter at that eye-position (Appendix, Eq. A20). Thus in Fig. 10B, the iso-position lines are for the most part straight and parallel. They are crossed, obviously not at right angles, by the curve showing the “reciprocal innervation” relation between the two innervation parameters (Appendix, Eq. A17). Comparison of Figs. 9 and 10B helps clarify a potential source of confusion created by use of the term “innervation parameter”: it does not refer to the motor command sent to the muscle (interpreted here as summed OMN firing rates) but to the combined effects of the motor command with muscle strength at that eye position (cf. Methods, Eq. 11). Although a given change in innervation parameter could be achieved solely by change in motor command (by keeping muscle strength fixed), in general the effect of recruitment is to change both motor command and muscle strength simultaneously. Figure 10B can be taken to illustrate the results of keeping muscle strength fixed, so that the innervation parameter does indeed simply reflect the motor command. Minimum-norm control is not achieved in these circumstances.

Fig. 7. A: isometric force gradients for the horizontal recti, using the equation and parameter values from Robinson (1975). Curve for the lateral rectus shows, for each position of the eye, how the force exerted by the muscle increases with fixation command when muscle length is held fixed at that position. Curve for the medial rectus muscle is reversed in sign. B: ratio of the isometric gradients shown in A, plotted on a logarithmic scale.
Data sets for OMN firing rates

The fit illustrated in Fig. 8 between the predictions from OMN firing rates and the data for isometric-force gradients of the horizontal recti was obtained with firing rates taken from the data set of Van Gisbergen and Van Opstal (1989). It is important to know how robust is the fit in Fig. 8 to variations in firing-rate data. For this purpose, four additional data sets were investigated, as explained in METHODS. The summed firing rates for three of these sets are plotted in Fig. 11A, together with the original data from Van Gisbergen and Van Opstal’s review. The remaining data set (from the review of Keller 1981) is not shown here on account of its close similarity with the data from Van Gisbergen and Van Opstal. In Fig. 11A, the summed firing rates have been normalized, that is, divided by the number of OMNs in that particular set of data. For eye positions less than about $215^\circ$, the summed firing rates for two of the distributions (King et al. 1981; Van Gisbergen and Van Opstal 1989) differ noticeably from the firing rates for the remaining two (Fuchs et al. 1988; Gamlin and Mays 1992). This difference between the two pairs of distributions is seen more clearly in Fig. 11B, which shows the percentage of low threshold units between the two sets of distributions. This difference is also apparent in the summed, normalized firing-rate gradients (Fig. 12A), and correspondingly in the squared ratio of those gradients (Fig. 12B). Comparison of those ratios with the ratio of isometric-force gradients derived from Robinson (1975) indicates that the region of reasonable fit (errors $\leq 0.01$) was similar to that of Van Gisbergen and Van Opstal for the distributions with appreciable numbers of low
threshold units: $\pm 37^\circ$ (King et al. 1981); $\pm 32^\circ$ (Keller 1981).

However, for the distribution of Gamlin and Mays (1992) the region of fit was about $\pm 15^\circ$, and there was no fit at all with the distribution of Fuchs et al. (1988).

The fit between data and minimum-norm prediction illustrated in Fig. 8 thus is influenced strongly by which set of experimental results are taken for the comparison. A major factor influencing the outcome is the proportion of low-threshold OMNs in the sample, though the difference in fit between the data set of Gamlin and Mays (1992) and that of Fuchs et al. (1988) indicates that the pattern of recruitment at higher thresholds is also influential.

**FIG. 10.** A: fixation command sent to 1 horizontal rectus muscle plotted against that sent to the other. Iso-position lines as in Fig. 9. Values calculated using a variant of the Robinson (1975) model in which the lateral and medial rectus are assumed to be identical (see METHODS). $\cdots$ connects the actual fixation commands used in the normally functioning eye (cf. Fig. 6A) and does not cross the iso-position lines at right angles (except for the line representing the primary position). B: plot as in A, except for innervation parameters $e$ in place of fixation commands. $\cdots$, connects the actual innervation parameters used in the normally functioning eye (cf. Fig. 6A) and does not cross the dotted lines at right angles (with the exception of the line representing the eye position $= 0^\circ$).

**FIG. 11.** A: summed firing rates for 4 samples of primate OMNs: F88 (n = 81) from Fuchs et al. (1988); vG89 (n = 87) from Van Gisbergen and Van Opstal (1989); K81 (n = 78) from King et al. (1981); G92 (n = 74) from Gamlin and Mays (1992). Sample details are given in METHODS. The summed firing rates for each sample have been normalized by dividing the raw sum of the firing rates by the number of units in the sample. B: thresholds for units in 4 samples of primate OMNs. Four samples have been aggregated into two groups: vG89 and K81 and F88 and G92. Graph shows, for each group, the percentage of units with thresholds in a $10^\circ$ range centered on the value given on the $x$ axis. In the case of the $-45^\circ$ value, all units with thresholds less than $-40^\circ$ are included. Two groups differ markedly in the proportion of units recruited in this range.
Variation of muscle parameters

The length-tension curves for extraocular muscle can be approximated by Eq. 1 of Robinson (1975), which contains the three parameters $k$, $a$, and $e$. The fit between prediction and data illustrated in Fig. 8 was obtained using a particular set of values for these parameters for medial and lateral recti (Robinson 1975). However, because a number of other values subsequently have been proposed, it becomes important to know the robustness of the fit in Fig. 8 to variations in parameter values. This section first considers variations in individual parameters (see METHODS).

PARAMETER $k$. This parameter controls the slope of the length-tension curves when the muscle is stretched (Fig. 1). Doubling or halving its value in both muscles changed the error scores (cf. Fig. 8B) by $<10\%$ over the eye-position range $\pm 30^\circ$ (not shown). This is because $k$ affects the isometric-force gradient in each of the two horizontal recti, so that the ratio between the two gradients is little altered (APPENDIX: Isometric force gradient with respect to fixation command). When the stiffnesses of the lateral and medial recti were made identical (Clement 1987; Simonsz and Spekreije 1996) there is a $40\%$ reduction in the already low error scores within the $\pm 30^\circ$ range of eye positions (not shown). This is perhaps not surprising in view of the assumption that the firing rates of the two OMNs were identical. However, the range of eye positions over which the errors remained small ($\leq 0.01$) stayed at about $\pm 32^\circ$.

PARAMETER $a$. This parameter controls the slope of the length-tension curves (Fig. 1). Doubling or halving the value of $a$ in both muscles alters the error score by $<10\%$ over the eye-position range $\pm 30^\circ$ (not shown). The reason for the relative insensitivity of the isometric-force gradient to the curvature parameter can be deduced from Fig. 5A: the natural operating region of the horizontal recti is where the length-tension curves are fairly linear (cf. Collins 1971).

PARAMETER $e$. This parameter controls the spacing of the length-tension curves that correspond to different values of the fixation command. A variety of relations between the parameter $e$ and the fixation command $\psi$ have been proposed (see METHODS). However, these appear to have little effect on the goodness of fit between isometric-force and firing-rate gradients. For example, one curious feature of the original model is the use of “secondary innervation.” If values for $e$ are taken from the original length-tension measurements (so-called primary innervation), the difference in force produced by the two muscles acting in concert is close to zero (APPENDIX, Fig. A1). The extra secondary innervation is needed to provide sufficient force to offset the passive torque of the orbital tissues, as described in INTRODUCTION. However, substituting the original estimates of the parameter $e$ have little effect on the ratio of isometric-force gradients, slightly reducing the range of eye positions giving a good fit to about $\pm 25^\circ$ (not shown). This is true for primary innervation values calculated either from Robinson (1975) or from Robinson (1981). A second example comes from Clement (1985), who suggested a slightly different equation for secondary innervation (see METHODS). The effects of this alteration on the isometric-force gradient for an individual muscle is shown in Fig. 13A, and on the ratio of the gradients for the two horizontal recti in Fig. 13B. Clement’s suggestion improves the errors within the eye-position range $\pm 30^\circ$ by $\sim 60\%$ but has very little effect on the range over which the good fit is obtained.
In addition to alterations in individual parameters, the effects on isometric-force gradient of more complex parameter variations were examined (see METHODS).

1) Isometric-force gradients obtained from the full three-dimensional model (cf. Miller and Shamaeva 1995) produced only a small (15%) increase in errors over the range of eye positions 630° (not shown). This result is consistent with the assumption that the horizontal eye muscles function fairly independently over this oculomotor range and suggests that the simplifications concerning the precise actions of the EOMs (see METHODS) are not important in the present context.

2) The worst fit between data and prediction was obtained from the measurements of Collins et al. (1975) (see METHODS). The isometric-force gradients for the horizontal recti are clearly different from those obtained with the other models (Fig. 13A), and the region of good fit (error 60.01) between muscle data and OMN firing rate is diminished to about 612°. This lack of fit is not improved by using a different data set for OMN firing rates: comparison of Fig. 13B with Fig. 12B indicates that the errors will add rather than cancel.

3) The final muscle variant to be investigated was based on the data of Simonsz (e.g., Simonsz and Spekreise 1996). As explained in METHODS, the model derived from this data sets the fixation command to zero at 30° in the OFF direction so that it cannot be used directly to compute isometric-force gradients outside that region. The strategy used here therefore was to calculate length-tension curves from the firing-rate data of Van Gisbergen and Van Opstal (1989), assuming that the length-tension curve for a fixation command of 15° in the OFF direction was linear and that the length-tension curves for smaller fixation commands were adjusted to fit the firing-rate predictions (details in APPENDIX: Minimum-norm equations for muscle). The shape of the length-tension curves so obtained is shown in Fig. 14A, and the corresponding fit between muscle “data” and firing-rate prediction illustrated in Fig. 14B. It can be seen that the effect of imposing the fit seen in Fig. 14B is to increase tension values for stretched muscle lengths (less than 10°) and low fixation commands (less than 15°). The new length-tension curve for fixation command equals 45° is fitted approximately by an exponential function. Thus the firing-rate prediction gives an exponential passive curve, together with a linear function for 615°, in qualitative agreement with the data in Simonsz and Spekreise (1996). In summary, variants in the values of muscle parameters that are based on the original measurements used by Robinson (1975) give very similar ratios of isometric-force gradients to those illustrated in Fig. 7B. The fit between data and minimum-norm prediction over an oculomotor range of 625–30° is therefore relatively insensitive to those variations. However, the parameters derived from the measurements of Collins et al. (1975) produce a fit only over a much reduced oculomotor range (612°). In contrast, a good fit over a 645° oculomotor range appears to require an exponential relationship between tension and length for passive muscle, similar to that measured by Simonsz (e.g., Simonsz and Spekreise 1996).

Estimation of muscle strength \( z \)

Muscle strength \( z \), as defined by Daunicht and interpreted here, is the increase in isometric force produced by unit increase in motor command \( \delta m \). Its value for a particular position of the eye depends on the average strength of the motor units that are recruited in that position (METHODS, Eq. 14). As such, \( z \) is not simply an intrinsic property of the muscle itself but also is influenced by the order in which motor units are recruited as the fixation command increases in magnitude. Altering the

FIG. 13. A: isometric-force gradients in the horizontal rectus muscle plotted against eye position for 3 sets of parameter values (details in text). R75 is for values from Robinson (1975), cf. Fig. 7A; CL85 is for values from Clement (1985); CO75 is for values from Collins et al. (1975). B: comparison of the ratio of isometric-force gradients from A with the square of the ratio of summed firing-rate gradients of a sample of OMNs described in Van Gisbergen and Van Opstal (1989). These 2 quantities should be equal at all eye positions if the oculomotor control system uses the minimum-norm rule. Muscle parameters suggested by Clement (CL85) gives a similar fit to the OMN curve as do the parameters of Robinson (R75). The fit for Collins’ parameters (CO75) is substantially worse.
structure of the fixation command thus could alter the value of \( z \). Consequently \( z \) cannot be measured directly by electrical stimulation of the motor nerve, because such unphysiological stimulation lacks the organization of the natural fixation command. However, it is possible to estimate \( z \) indirectly from direct measurements, by dividing the isometric-force gradient at a given eye-position by the summed firing-rate gradient at that position (METHODS, Eq. 11). These estimates are shown in Fig. 15, for four different combinations of force and firing-rate measurement.

The two curves in Fig. 15A illustrate how \( z \) varies with eye position for two data-set combinations that produced a good fit between data and minimum-norm prediction. One curve is for a variant of the “basic” combination, of firing rates from the review of Van Gisbergen and Van Opstal (1989) with isometric force from the model of Robinson (1975) with identical horizontal recti (Clement 1987). This combination produces a reasonable fit with the minimum-norm prediction over the eye-position range \( \pm 30^\circ \). For eye positions greater than \(-30^\circ\), \( z \) increases monotonically with eye position. At \(-30^\circ\), however, \( z \) increases as eye position decreases, producing an overall U-shaped curve. Thus the region of good fit to the minimum-norm prediction coincides with the region in which \( z \) increases with eye position in the ON direction for both muscles. This is also the case for the second curve shown in Fig. 15A, which is for the same firing-rate data (Van Gisbergen and Van Opstal 1989) together with the EOM length-tension relations illustrated in Fig. 14A. By design, this combination produces a good fit over the entire oculomotor range (Fig. 14B). As Fig. 15A shows, it also produces values for \( z \) that increase as eye position increases over the full \( \pm 45^\circ \) range of eye positions.

In contrast, the two curves of Fig. 15B show how \( z \) varies with eye position for two data-set combinations that produced a poor fit between data and minimum-norm prediction. One curve is for the same firing-rate data shown in Fig. 15A (Van Gisbergen and Van Opstal 1989), together with isometric force estimates from the data given by Collins et al. (1975). The curve shows \( z \) decreasing with eye position up to about \(-10^\circ\), then increasing slightly. The region of fit between data and minimum-norm prediction for this combination of data were about \( \pm 10^\circ \) (Fig. 13B). Finally, the remaining curve in Fig. 15B is for firing-rate data from Fuchs et al. (1988) together with the isometric force from the model of Robinson (1975). This combination produced no region of fit between data and prediction, and correspondingly in Fig. 15B \( z \) starts to increase with eye position only for positions greater than about \( +5^\circ \). There is no range of eye positions for which \( z \) increases with ON direction for both muscles.

These results show how implementation of minimum-norm control requires the appropriate recruitment of EOM motor units. In particular, it requires that the muscle strength \( z \) should increase as eye position moves into the ON direction of the muscle. Given the interpretation of muscle strength adopted here, this in turn means that motor units have to be recruited in order of increasing strength. Thus an important and possibly unexpected corollary of minimum-norm control in the oculomotor system is that it appears to require the “size principle” of motor unit recruitment (e.g., Henneman and Mendell 1981; Henneman et al. 1965).

**DISCUSSION**

The question addressed in this study was whether the control system for horizontal eye position used the minimum-norm principle, as formulated by Daunicht (1988, 1991), to determine the forces exerted by the horizontal recti. To answer the question, data on the summed firing-rate gradients of OMN pools in primate were compared with data on the isometric-
The results of the comparison can be summarized as follows. There was good agreement between the minimum-norm prediction and experimental observation over about a 6°–30° range of eye positions for the pair of data sets selected as representative. This fit was robust with respect to variations in muscle stiffness and in methods of calculating muscle innervation.

Other pairs of data sets gave different estimates for the range of eye positions within which the minimum-norm prediction held. These estimates varied from 0° (that is, no fit at all) to 6°–45° (essentially the full oculomotor range).

For each pair of data sets, the range of eye positions over which the minimum-norm rule applied was determined by the pattern of motor unit recruitment inferred for that pair. It corresponded to the range of eye positions over which the size principle of recruitment was obeyed by both agonist and antagonist muscles.

These findings raise the following issues for discussion: the origin of the differences between the data sets, a possible rationale for the implementation of minimum-norm control, and the implications of its implementation.

Differences between data sets

Measurements of OMN firing rates. The success of the minimum-norm rule in predicting experimental results was affected markedly by the origin of the data for the summed OMN firing rates. When compared with isometric-force gradients derived from the length-tension measurements incorporated in the original Robinson model (Robinson 1975), three of the OMN samples gave reasonable fits over at least a ±30° range of eye positions, one gave a fit over ±15°, and one gave no fit at all (Fig. 12B). Goodness of fit was related to the proportion of OMNs in a sample with thresholds less than 2° (e.g., Fig. 11B). The two populations of OMNs containing ≥1% of these units gave poor fits to the minimum-norm prediction, whereas the three populations containing >10% of such units gave better fits. The important issue, therefore, is the origin of these differences in the proportion of low-threshold units.

One of the data sets with few low-threshold OMNs (lowest threshold 1°, 74 units) was obtained by Gamlin and Mays (1992), from a sample of medial rectus motoneurons (MR-MNs). It has been suggested that there may be particular difficulties in obtaining a representative sample of MR-MNs (e.g., Dean 1997) because of the way in which they are distributed within the primate oculomotor nucleus. MR-MNs are found in three spatially separated clusters (Büttner-Ennever and Akert 1981; Spencer and Porter 1981). One of these clusters, termed subgroup C by Büttner-Ennever and Akert (1981), lies dorsomedially outside the classical borders of the oculomotor nucleus and is likely to be underrepresented unless special steps are taken to sample it. Subgroup C has a number of distinctive characteristics. It contains relatively small neurons, which receive distinctive inputs, and its motor units are located within the orbital layer of the medial rectus muscle and contain multiply innervated fibers (Büttner-Ennever and Akert 1981; Büttner-Ennever et al. 1996, 1998). Because there is evidence suggesting that the first motor units to be recruited contain multiply innervated fibers and are located in the orbital

![Fig. 15. A: muscle strength plotted against eye position for 2 combinations of data that gave a good fit for the minimum-norm prediction. CL87-vG89: muscle parameters from a variant of the Robinson (1975) model in which the lateral and medial rectus are assumed to be identical (Clement 1987), OMN sample from Van Gisbergen and Van Opstal (1989). S96-vG89: muscle parameters as in Fig. 14A; these parameters are similar to those of Simonsz and Spekreise (1996), OMN sample from Van Gisbergen and Van Opstal (1989). Muscle strength z at a given position of the eye is the ratio of the isometric-force gradient to the firing-rate gradient at that position. Firing-rate gradients are normalized, that is, the total firing rate for the sample is divided by the number of units in the sample (cf. Fig. 12A). B: muscle strength plotted against eye position for two combinations of data that gave a poor fit for the minimum-norm prediction. CL87-F88: muscle parameters from a variant of the Robinson (1975) model in which the lateral and medial rectus are assumed to be identical (Clement 1987), OMN sample from Fuchs et al. (1988). CO75-vG89: muscle parameters from Collins (1975), OMN sample from Van Gisbergen and Van Opstal (1989).]
layer (summarized in Dean 1996), a sample of MR-MNs in which subgroup C was underrepresented could well contain a disproportionately small percentage of low-threshold OMNs.

The remaining data set with few low-threshold neurons was that of Fuchs et al. (1988). In this sample of 81 units from the abducens nucleus, the lowest threshold found was about $-38^\circ$. The procedure used to obtain the sample was quite different from those used in other studies of OMN firing rates. A unit was only included in the sample if its action potentials triggered averages of EMG activity recorded from indwelling electrodes in the lateral rectus muscle. This requirement ensured that lateral rectus motoneurons (LR-MNs) could be distinguished from other neurons within the abducens nucleus, particularly those projecting to the contralateral MR-MNs (abducens interneuronal neurons). Previous studies, including those contributing to the data sets of Keller (1981) and Van Gisbergen and Van Opstal (1989), did not make this distinction. However, comparison of the proportion of recorded abducens neurons identified as LR-MNs using the EMG technique with the proportion estimated anatomically suggested that the technique correctly identified, on average, 58–88% of the MNs (Fuchs et al. 1988). Moreover, because it was ‘‘possible that the EMG technique did not detect potentials from small or nonspiking muscle fibers’’ (Fuchs et al. 1988, p. 1,889), the overlooked LR-MNs might have contained a high proportion of low-threshold units. Finally, recent evidence indicates that the motoneurons that innervate multiply innervated fibers within the lateral rectus muscle lie just outside the boundary of the classical abducens nucleus (Büttner-Ennever et al. 1998).

Thus plausible reasons can be offered for why both the OMN samples that contained few low-threshold units were biased. Unfortunately, the samples containing higher proportions of such units also give cause for concern. One sample contained OMNs responsible for vertical rather than horizontal eye position (King et al. 1981). The other two samples pooled from those used in other studies of OMN firing rates. A unit was only included in the sample if its action potentials triggered averages of EMG activity recorded from indwelling electrodes in the lateral rectus muscle. This requirement ensured that lateral rectus motoneurons (LR-MNs) could be distinguished from other neurons within the abducens nucleus, particularly those projecting to the contralateral MR-MNs (abducens interneuronal neurons). Previous studies, including those contributing to the data sets of Keller (1981) and Van Gisbergen and Van Opstal (1989), did not make this distinction. However, comparison of the proportion of recorded abducens neurons identified as LR-MNs using the EMG technique with the proportion estimated anatomically suggested that the technique correctly identified, on average, 58–88% of the MNs (Fuchs et al. 1988). Moreover, because it was ‘‘possible that the EMG technique did not detect potentials from small or nonspiking muscle fibers’’ (Fuchs et al. 1988, p. 1,889), the overlooked LR-MNs might have contained a high proportion of low-threshold units. Finally, recent evidence indicates that the motoneurons that innervate multiply innervated fibers within the lateral rectus muscle lie just outside the boundary of the classical abducens nucleus (Büttner-Ennever et al. 1998).

For the short term, there is one additional observation that is especially relevant to the present study, which concerns EMG activity in human horizontal recti (Collins 1975). Recordings with a multiple electrode array showed clear EMG activity in the orbital layer at 40 and 50° in the OFF direction of the muscle (Fig. 5 of Collins 1975). These results suggest either that the primate OMN samples with no units firing at these eye positions are indeed unrepresentative or that in this particular regard humans differ from monkeys (despite general similarities) (e.g., Trimble et al. 1974). In the present context, therefore, the human EMG measurements appear to favor these OMN samples that gave a reasonable fit to the minimum-norm prediction over about $\pm 30^\circ$.

MEASUREMENTS OF EOM LENGTH-TENSION CURVES. The success of the minimum-norm rule in predicting experimental results [using firing-rate data from Van Gisbergen and Van Opstal (1989)] was in some respects very robust to variations in EOM length-tension curves. As explained in METHODS, length-tension curves usually are specified by three parameters, related to stiffness, ‘‘curvature,’’ and innervation. A fit to the minimum-norm prediction over about a $\pm 30^\circ$ range of eye positions was obtained with muscle parameters derived from the length-tension measurements summarized in Robinson (1975). These were from the horizontal recti of strabismic patients (Collins 1971; Collins et al. 1969; Robinson et al. 1969), described as an ‘‘average of all results to date provided by C. C. Collins and D. M. O’Meara’’ (Robinson 1975), and are the basis for the models of Robinson (1975, 1981), Miller and Robinson (1984), and Miller and Shamaeva (1995). The fit to minimum-norm prediction was little affected either by substantial variations in the muscle stiffness and curvature parameters including those related to symmetry or by the changes in innervation parameter produced by different estimates of its relation to fixation command or by implementation of a full three-dimensional EOM model (see RESULTS). The relative insensitivity of the fit to these variations is important given the possible problems associated with data obtained from muscles in strabismic patients.

There were, however, two other sets of measurements that did alter the fit between data and minimum-norm prediction. When the comparison with firing-rate data was made with muscle parameters derived from the measurements of Collins et al. (1975), the range of fit was reduced to about $\pm 10^\circ$. The measurements taken by Collins et al. (1975) were from muscles with an implanted force transducer (see Estimation of isometric force gradients). The primary purpose of the implantation procedure was to investigate the dynamic forces of the muscles during movements of the eye, and precise values for static forces may have been distorted. One reason for considering this possibility is the unusual nature of the best-fit equation that relates innervation parameter to fixation command for Collins et al.’s measurements. In contrast to the equations derived from Robinson’s (1975) measurements, which require cubic or quartic terms (Eqs. 16, A14), the equation for Collins et al. is a quadratic (Eq. 17). This is interesting for two connected reasons. First, a similar relationship was observed for cat (Collins 1971) for artificial stimulation of the motor nerve. Artificial stimulation differs crucially from the natural fixation command in not having any recruitment. All units are activated by the stimulation so that muscle strength $z$ is fixed at its highest possible value (see Interpretation and measurement of $z$). Second, the gradient of a quadratic curve is linear, giving rise to the near-linear relation of isometric-force gradient to eye position derived from measurements by Collins et al. (Fig. 13A). Because the firing-rate gradient for OMNs is also fairly linear over part of the oculomotor range, (e.g., Fig. 6B), the quantity $z$, which relates isometric-force gradient to firing-rate gradients (Eq. 11), is nearly constant over that range (cf. Fig. 15B). Thus two kinds of evidence suggest that the method used by Collins et al. artificially stabilized muscle strength. It is possible that this effect is related to disturbance by the transducer of the relation between eye position and muscle length, if, for example, the measured muscle was relaxed by the diameter of the transducer plus the lengths of the attaching sutures. In any event, measurements obtained by a method that stabilized muscle strength would have disadvantages for testing whether minimum-norm control is used under normal circumstances.

The second alteration in fit between data and prediction was related to measurements of the behavior of passive (i.e., not...
innervated) muscle when it is stretched. The family of hyperbolic curves fitted by Robinson (1975) all have the same stiffness, that is, the slope of the length-tension curve for stretched muscle is not altered by innervation. In contrast, Simonsz and coworkers found that the linear length-tension relation for innervated muscle was replaced by an exponential relationship for passive muscle (e.g., Simonsz and Spekreijse 1996). Because this difference between passive and innervated muscle compresses the length-tension curves for muscle at low levels of fixation command at extreme eye positions (cf. Fig. 14A), the isometric-force gradients at extreme eye positions are reduced. This should bring the behavior of the muscle more into line with the prediction of minimum-norm control, and indeed working backward from that prediction (see METHODS) shows that if it is obeyed over the entire oculomotor range (±45°), the resultant length-tension curve for passive muscle has an exponential shape qualitatively similar to the measurements of Simonsz (Fig. 14). The existence of exponential shaped curves for passive EOM appears not to be in doubt, as they have been observed both in primate (Fuchs and Luschei 1971) and in cat (Collins 1971), and Miller and Robinson (1984) state that “if a (human) muscle is stretched sufficiently, a point is reached at which stiffness increases dramatically.”

The key issue is a quantitative one, concerning the actual position of the eye at which the nonlinearity first appears. Miller and Robinson’s measurements indicate that this point is ~50° in the off direction for normal horizontal rectus muscle, whereas the measurements of Simonsz and coworkers give a value of ~27° (Simonsz and Spekreijse 1996). Although the issue is a quantitative one, its resolution may have qualitative implications for motor-unit recruitment. Simonsz and Spekreijse’s value of ~27° is consistent with motor unit recruitment according to the size principle over the entire oculomotor range (Fig. 15A), whereas the ~50° value of Miller and Robinson requires the earliest recruited units to be stronger than those recruited later, giving rise to a U-shaped plot of muscle strength z against eye position (Fig. 15, A and B). A previous modeling study of motor-unit recruitment (Dean 1996) also found a U-shaped pattern of motor-unit strength as a function of OMN threshold, which appeared very robust with respect to assumptions concerning possible distributions of OMN parameters and the relation between OMN firing rate and unit force. However, the study did not explore the particular possibility that is required by the data of Simonsz and Spekreijse. To produce the curves shown in Fig. 14A, the active force produced by the earliest recruited units has to decline as the muscle is stretched, whereas the active force produced by the later recruited units needs to increase with stretch. At present, initial evidence from direct measurements of EOM motor units (Goldberg et al. 1997b) suggests that their twitch tensions vary similarly with muscle length. The source of this possible discrepancy is not known.

In summary, there seem to be difficulties with the length-tension measurements of EOM that give estimates differing from ±30° for the oculomotor range over which minimum-norm control might apply. The low estimate of ±10° may derive from distortions introduced by implanted force transducers (Collins et al. 1975), whereas the high estimate of ±45° appears to require unrealistic motor unit behavior. Therefore ±30° may be taken as the best currently available estimate of the minimum-norm control range, with the strong proviso that the behavior of EOM at extreme off positions is not well understood.

Rationale for minimum-norm control

The purpose of the present study was simply to compare the predictions of the minimum-norm rule with relevant data: the possible theoretical basis of the rule itself was the subject of a companion modeling study (Dean and Porrill 1998). Nonetheless, interpretation of the comparison’s outcome raises a theoretical question that requires consideration here.

The question is whether there is a compelling rationale for minimum-effort control or whether there are alternative minimization rules that would fit the data just as well. Simple minimization of the energy spent in either neural firing or muscular contraction seems not to be a plausible alternative given the activity observed in what might have been a resting state with the eye, namely the primary position (see INTRODUCTION). About 80% of OMNs fire in the primary position (e.g., Keller 1981), and many EOM fibers demonstrate specialized metabolic adaptations for continuous activity (e.g., Porter et al. 1995).

These data suggest that energy is being killed for some other functional consideration. In the case of muscles specialized for controlling the position of the eye, an obvious possibility is stability of the visual image. Is there any connection between minimum-norm control and the reduction of image movements that would disturb visual processing? The connection suggested by the companion modeling study is as follows.

OMN firing rates are assumed to be noisy. The effects of this noise on eye position will depend on the strength of the motor unit that the OMN controls: the stronger the unit, the greater the image movement induced by OMN noise. To minimize image movement, the control system must therefore learn to recruit weak motor units before strong ones, so implementing the size principle (cf. Senn et al. 1997).

Because OMNs with higher thresholds have greater firing-rate slopes (see Interpretation and measurement of 8m), stronger motor units are in effect given larger changes in motor command: this particular implementation of the size principle gives a close approximation to minimum-norm control (Dean and Porrill 1998).

There is evidence in favor of each of the links in this chain connecting image stability to minimum-noise control. Variability in OMN firing-rates has been observed in cat (Gomez et al. 1986) and primate (Goldstein and Robinson 1986). The maintenance of accurate position commands to OMNs generally is recognized to require some form of calibration, especially in the face of naturally occurring alterations to crucial variables such as overall muscle strength or vestibular input (Berthoz and Melvill Jones 1985; Grossberg and Kuperstein 1989). Inaccurate position commands give rise to post-saccadic drift of the eye (e.g., Optican and Robinson 1980), and artificially induced drift produces changes in position command (Optican and Miles 1985). Moreover, it appears that different position commands can be sent to motor units of differing strength. A simulation study of the recruitment pattern of medial rectus motoneurons (Dean 1997) indicated that it was unlikely to be the result of a common motor command acting equally on motoneurons which varied in threshold.
Rather, the recruitment pattern appeared to arise, at least in part, from different OMNs receiving different synaptic inputs.

It can be seen from the results plotted in Fig. 15 of the present study that, whether a particular combination of data sets gives a good or a poor fit to the minimum-norm prediction, there is a close relationship between the range of eye positions giving the fit, and the range over which muscle strength \( z \) increases monotonically with \( \text{ON} \) direction eye position for both horizontal recti. The relationship follows from the fundamental requirement of minimum-norm control that change in motor command be matched to muscle strength (Fig. 3). Because the gradient of summed OMN firing rates increases with eye position, one way of achieving the match is to have muscle strength increase also. Given the simplifying assumptions described in METHODS (Interpretation and measurement of \( z \)), the only way a muscle can increase its strength is to recruit stronger motor units. Thus there appears to be a fundamental connection between the size principle of motor unit recruitment and minimum-norm control.

In addition, the optimization of image stability may be consistent with the apparent restriction of minimum-norm control to a central region of the oculomotor range if it is the case that the first motor units to be recruited consist of multiply innervated fibers (Dean 1996). It has been suggested that multiply innervated fibers are a functional specialization of EOMs designed to minimize fluctuations in muscle force (Robinson 1978). If so, the contribution to noise-induced image drift of a unit containing these fibers would be less than that of a conventional unit of identical strength. The learning mechanism for calibrating the position command therefore would allow such units to be stronger than subsequently recruited conventional units, giving rise to a U-shaped recruitment pattern (Fig. 15) and the corresponding restriction on minimum-norm control.

There is thus a variety of evidence apparently consistent with the suggestion that the approximation to minimum-norm control observed in the present study arises from optimization of retinal-image stability, using a distributed system of noisy motor units of differing strengths. However, crucial evidence concerning the relationship of OMN firing-rate threshold to motor unit strength, and the precise functional nature of different types of EOM fiber, are not currently available (issues briefly reviewed in Dean 1996).

Implications

The horizontal recti in people exert \( \sim 10 \text{ g} \) of force in the primary position. The question posed in the Introduction was how this value was determined by the oculomotor control system. The present results suggest the possible explanation that it arises from a combination of the minimum-norm rule and the size of the oculomotor range. The minimum-norm rule itself requires only that the motor-command values lie on a line at right angles to the iso-position lines (Fig. 3B), not specifying any particular crossing point. But once the ends of the motor-command line are fixed by the oculomotor range (cf. Fig. 9), then the whole line is fixed. The value of 10 g is thus the least force that is compatible with minimum-norm control and an oculomotor range of about \( \pm 45^\circ \). One implication of this suggestion is that variations in the size of oculomotor range between species (e.g., Barmack 1982), or within species at different stages of development, should correlate with the variations in active muscle force at the primary position.

A more significant implication of the minimum-norm rule concerns the control of eye-position in three dimensions. The model described by Daunich (1988, 1991) is for three-dimensional control (cf. APPENDIX: Pseudoinverse control) and addresses a problem not considered in the present study, namely the coordination of muscles of markedly different strength. Initial results (Warren et al. 1998) suggest that it is compatible with current mechanical models of the six EOMs (e.g., Miller and Shamaeva 1995). Such compatibility may be of clinical relevance. A control system using the minimum-norm rule will adjust its command signals in response to a change in muscle strength. The effects of, for example, strabismus surgery therefore will include not only direct changes in muscle mechanics but also the consequent changes in motor command. An understanding of minimum-norm control therefore might assist in the prediction of surgical outcomes.

Finally, it has been observed that the position-related firing rates of OMNs vary with vergence state (e.g., Gamlin and Mays 1992; Gamlin et al. 1989, 1994; King et al. 1994; Mays and Porter 1984). Although recent data obtained with implanted force transducers indicate that conduction does not occur during vergence displacements (Miller 1998), the possibility of minimum-norm violation associated with vergence is an important issue for further investigation.

APPENDIX

Derivation of minimum-norm rule for horizontal eye position

The first step is to determine the relationship between the motor commands \( m_1 \) and \( m_2 \) sent to the horizontal recti and the resultant position \( \phi \) of the eye. This can be regarded as the forward control equation for horizontal eye position. Because muscle force is a nonlinear function of length and motor command, the problem is linearized by dealing with the change in eye position \( \delta \phi \) that results from small changes in motor command \( \delta m_1 \) and \( \delta m_2 \). If we take an individual muscle with command \( m_\alpha \) and length \( \rho_\alpha \), corresponding to eye position \( \phi \), Taylor’s expansion gives

\[
\delta f(m, p) = \delta f(m_\alpha, p_\alpha) + \frac{\partial f}{\partial m} \delta m + \frac{\partial f}{\partial p} \delta p + O(\delta m, \delta p)^2
\]

where \( \delta f(m, p) \) is the force exerted by the muscle at a new command \( m \) and length \( p \) and is the force exerted by the muscle at the original command and position. By making the quantities \( (m - m_\alpha) \) and \( (P - \rho_\alpha) \) very small, their squares and higher powers can be ignored

\[
\delta f(m_\alpha, \rho_\alpha) = \frac{\partial f}{\partial m} (m_\alpha, \rho_\alpha) \delta m + \frac{\partial f}{\partial \rho} (m_\alpha, \rho_\alpha) \delta \rho
\]

where

\[
\delta f = f(m, p) - f(m_\alpha, \rho_\alpha) \\
\delta m = m - m_\alpha \\
\delta \rho = p - \rho_\alpha
\]

The change in muscle force \( \delta f \) has two components, an active one due to change in motor command and a passive one due to change in length. Equation A2 gives the same relationship in terminology similar to that of Daunich (1991).

\[
\delta f = \hat{z} \delta m + \hat{\xi} \delta \rho
\]
The term \( z \) thus denotes the isometric-force gradient of the muscle with respect to motor command (measured as force per unit change in motor command), and its stiffness (measured as force per unit change in length). As the notation of \( \delta m \) emphasizes, their values are not constant but are functions of the starting conditions \( m_0 \) and \( \phi_0 \).

In the case where two motor commands, \( \delta m_1 \) and \( \delta m_2 \), produce force changes \( \delta f_1 \) and \( \delta f_2 \), the resultant change in angle \( \delta \phi \) is

\[
\delta f_1 - \delta f_2 = L \delta \phi \quad (A4)
\]

where \( L \) is the coefficient of elasticity of the orbital tissues (measured as force per unit change in eye position) at eye position \( \phi \). Because \( \delta \phi \) is small, by Taylor's expansion \( L \delta \phi \) is a good approximation to the change in passive tissue force. The minus sign reflects the geometry of the eye muscles in relation to the eye: an increase in force by \( \delta f_1 \) produces a decrease in angle \( \phi \), given the definition that \( \phi \) increases to the left (Fig. 2B). Substituting Eq. A3 in Eq. A4 and rearranging

\[
z_1 \delta m_1 - z_2 \delta m_2 = -\xi_1 \delta \phi_1 + \xi_2 \delta \phi_2 + L \delta \phi \quad (A5)
\]

The relationship between the change in eye position and the change in lengths of the muscles again is determined by the geometry of the eye-rotation, the matrix \( MZ \) in Eq. A13 and rearranging

\[
z_1 \delta m_1 - z_2 \delta m_2 = (\xi_1 + \xi_2 + L) \delta \phi \quad (A6)
\]

in which the coefficients of muscle elasticity now are measured as force per unit change of eye position. This is Eq. 3 in METHODS and is the forward equation for control of horizontal eye position.

The inverse equation for control of horizontal eye position would give the commands \( \delta m_1 \) and \( \delta m_2 \) that were needed to produce a desired horizontal displacement \( \delta \phi \). As Eq. A6 shows, there is no unique solution to this problem, unless some additional constraint linking \( \delta m_1 \) and \( \delta m_2 \) is introduced. The constraint used here is that of minimum norm, where the norm \( N \) is a measure of the magnitude of the change in the two motor commands expressed as the vector \( (\delta m_1, \delta m_2) \) (cf. next section)

\[
N = \sqrt{(\delta m^2_1 + \delta m^2_2)} \quad (A7)
\]

This equation can be used to substitute for \( \delta m_2 \) in Eq. A6, producing

\[
z_1 \delta m_1 - z_2 \sqrt{N^2 - \delta m^2_1} = (b_1 + b_2 + L) \delta \phi \quad (A8)
\]

Equation A8 can be regarded as an expression giving the \( \delta \phi \) produced by any given \( \delta m_1 \) if \( E \) is fixed. To find the value of \( \delta m_1 \) that gives the maximum value of \( \delta \phi \), Eq. A8 can be differentiated and put equal to zero

\[
(b_1 + b_2 + L) \frac{d(\delta \phi)}{d(\delta m_1)} = z_1 + \frac{z_2 \delta m_1}{\sqrt{N^2 - \delta m^2_1}} = 0
\]

\[
z_1 = -\frac{z_2 \delta m_1}{\sqrt{N^2 - \delta m^2_1}} \quad (A9)
\]

Because the term is equal to \( \delta m_2 \), Eq. A9 is equivalent to

\[
z_1 = -\frac{z_2 \delta m_1}{\delta m_2}
\]

that is

\[
\frac{\delta m_1}{\delta m_2} = -\frac{z_1}{z_2}
\]

which is Eq. 5 in METHODS.

Finally, the relation between \( \delta m_1 \) and \( \delta m_2 \) that is imposed by the minimum-norm constraint can be used with the forward Eq. A6 to produce the inverse equations

\[
\delta m_1 = \frac{z_1}{z_1 + z_2} (\xi_1 + \xi_2 + L) \delta \phi
\]

\[
\delta m_2 = -\frac{z_2}{z_1 + z_2} (\xi_1 + \xi_2 + L) \delta \phi \quad (A10)
\]

These equations give the actual values required for minimum-norm control of horizontal eye position.

**Pseudoinverse control**

The forward Eq. A6 can be rewritten in matrix form as follows

\[
\begin{bmatrix} +1 & -1 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ z_1 & z_2 \end{bmatrix} = \begin{bmatrix} \delta m_1 \\ \delta m_2 \end{bmatrix} = (\xi_1 + \xi_2 + L) \delta \phi \quad (A11)
\]

This way of expressing the relationship between change in motor commands and change in angle of rotation draws attention to the geometric relationship between the muscles and the position of the eye referred to above, by placing it in the matrix \( [+1 -1] \). It also leads to a more general notation as used by Daunicht (1991), a version of which is

\[
MZ \delta m = S \delta e
\]

Here the changes in motor command are expressed as a two-dimensional vector \( \delta m \) and the change in eye rotation as a one-dimensional vector \( \delta e \). The geometric relationship between the extraocular muscles and eye rotation is now denoted by the \( 2 \times 1 \) matrix \( M \), the muscle strengths by the \( 2 \times 2 \) matrix \( Z \), and the various elasticities combined into the \( 1 \times 1 \) matrix \( S \) (which also incorporates the geometric relationship expressed by \( M \)). In this form, the forward control equation can be generalized to three dimensions.

The corresponding form of the inverse Eq. A10 is now

\[
\delta m = [MZ]^+ \delta e \quad (A13)
\]

Because there are more muscles than degrees of freedom for eye-rotation, the matrix \( MZ \) in Eq. A13 is asymmetrical and therefore does not have a proper inverse. The notation \([MZ]^+\) denotes the Moore-Penrose generalized inverse, which produces a matrix that minimizes the squared sum of the components of the command vector \( \delta m \) (i.e., minimum norm). This use of this inverse in artificial systems is referred to as pseudoinverse control (e.g., Klein and Huang 1983).

**Secondary innervation and the parameter \( e \)**

The values of \( e \) from Fig. 3 of Robinson (1975), which are derived directly from measurement of length-tension curves, are plotted as a function of fixation command \( \phi \) in Fig. A1A. This figure shows both the data points and the best fit cubic \((\cdot\cdot\cdot) \) to them

\[
e_a = 3.92 + 0.443\phi + 7.99 \times 10^{-3}\phi^2 + 8.89 \times 10^{-4}\phi^3 \quad (A14)
\]

The subscript \( dl \) means that the parameter \( e \) in Fig. 3 of Robinson (1975) is expressed as percentage change in muscle length rather than as the equivalent change in eye position.

The parameter values for \( k, a, \) and \( e \) from Robinson (1975) (see METHODS) then were incorporated into a computer simulation of the two horizontal recti. However, when the values of \( e \) shown in Eq. A14 were used in Eq. 1 to derive the forces exerted by both lateral and medial recti, the summed directional force of the two muscles was close to zero (Fig. A1B). It can be seen from Eq. 2 that this summed force is needed to balance the passive force exerted by the stretched orbital tissues; hence the values of \( e \) in Fig. A1A correspond to a situation where the orbital tissue forces are zero. Robinson (1975)
termed the values of muscle force at the primary position produced by these values of \( e \) primary innervation.

Values of \( e \) consistent with realistic values of the orbital tissue force were derived by Robinson (1975) as follows. The basic idea is to find two equations that link the innervation parameters \( e_1 \) and \( e_2 \) (for agonist and antagonist muscle, respectively) and then solve them. One of the equations is for the balance of forces (Eq. 2). Substitutions are made for each of the three terms in this equation. The muscle forces \( f_1 \) and \( f_2 \) are calculated from the basic muscle Eq. 1

\[
\frac{k_2}{2}(\phi - e_1) + \frac{k_1}{4}(\phi - e_1)^2 + a_1 - \frac{k_3}{2}(\phi + e_2) - \frac{k_4}{4}(\phi + e_2)^2 + a_2 = -F_{OT}(\phi) = 0 \quad (A15)
\]

The force \( F_{OT} \) exerted by the orbital tissues is given in Eq. 45 of Robinson (1975)

\[
F_{OT}(\phi) = 0.48\phi + 1.56 \times 10^{-4}\phi^4 \quad (A16)
\]

When this expression is substituted for the term \( F_{OT}(\phi) \) in Eq. A15, the first equation linking \( e_1 \) and \( e_2 \) is completed.

The second equation is

\[
e_1 = \frac{(h + w)^2}{(e_2 + w)} - w \quad (A17)
\]

This is Eq. 41 of Robinson (1975), and the values of \( h \) and \( w \) that fit experimental data are 4.0 and 9.7, respectively. It is possible to substitute for \( e_2 \) in Eq. A16, using Eq. A17, producing an equation in the variables \( \phi \) and \( e_1 \) only. This can be solved numerically, using routines in MATLAB. The resultant values of \( e_1 \) as a function of \( \phi \) can be fitted by a polynomial, shown in Fig. A1A. The values of \( e_2 \) can then be extracted from Eq. A17.

It can be seen from Fig. A1A that the new values for \( e \) are higher than the original values for \( \phi > 0 \); this difference, required to balance the passive forces of the orbital tissue, corresponds to the term secondary innervation of Robinson (1975). The best fit quartic curves to \( e_1 \) and \( e_2 \) are given in Eq. 16 in METHODS.

**Isometric force gradient with respect to fixation command**

The fixation command \( \psi \) does not appear directly in the length-tension curves of Eq. 1 but only indirectly as the innervation parameter \( e \). It is therefore necessary to apply the following chain rule

\[
\frac{\partial F}{\partial \psi} = \frac{\partial F}{\partial e} \frac{\partial e}{\partial \psi} \quad (A18)
\]

where \( \partial F/\partial \psi \) is the isometric-force gradient with respect to fixation command; \( \partial F/\partial e \) is the partial differential of Eq. 1 with respect to the innervation parameter \( e \); and \( \partial e/\partial \psi \) the differential of \( e \) with respect to the fixation command \( \psi \). Values for the terms on the right hand side of Eq. A18 can be derived analytically. Thus the expression for \( \partial F/\partial e \) is (cf. Eq. 50 of Robinson 1975)

\[
\frac{\partial F}{\partial e} = \frac{k}{2} - \frac{k_2}{4}(\phi + e)^2\left[\frac{k_1}{4}(\phi + e)^2 + a\right]^{-1/2} \quad (A19)
\]

and \( \partial e/\partial \psi \) can be obtained by differentiating the polynomials in Eq. 16 in METHODS. In practice, \( \partial F/\partial \psi \) was obtained by numerical differentiation.

Equation A19 can be simplified greatly if the effects of the \( a^2 \) term are negligible. In this case, the isometric-force gradient

\[
\frac{\partial F}{\partial \psi} = k \frac{\partial e}{\partial \psi} \quad (A20)
\]

Because the natural operating points of the muscle lie on fairly linear regions of the length-tension curves (Fig. 6A), the approximation of Eq. A20 is likely to be a useful one. This can be seen in Fig. 10B, which plots iso-position curves in terms of the innervation parameters for the two muscles. The curves are mainly linear and parallel, indicating that the innervation parameter has a fixed linear relation to muscle force.

**Minimum-norm equations for muscle**

It is possible to calculate length-tension curves for EOM that fit the predictions of minimum-norm control. In the method used here, the
predicted ratio of isometric-force gradients was derived from the summed firing rates of the OMN population described in Van Gisbergen and Van Opstal (1989), using Eq. 15. The muscle equations (with identical horizontal recti) (Clement 1987) then were adjusted to give this ratio. The adjustment was made for eye positions at 5° intervals from −10° to −50°. At each position, a ‘squashing’ parameter \( s \) was introduced, which altered the tension difference between the passive fixation command (assumed equal to −5°) and an unchanged −15° command (derived from Simonsz and Spekreije 1996). The relative spacing of the intermediate fixation commands (as determined by the parameter \( e \)) was maintained. The value of \( s \) that gave the required isometric-force gradient then could be calculated, using a bisection/interpolation algorithm (MATLAB). The calculated value of \( s \) then could be used to derive the tension values at each eye position for different values of fixation command. Finally, these tension values were used to plot the new length-tension curves (Fig. 14).

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REFERENCES


MILLER, J. M. AND SHMAIEVA, I. Orbit 1.5 Gaze Mechanics Simulation. Suite 404; 1450 Greenwich Street; San Francisco; CA 94109; Eidactics, 1995.


