

95 Neural Control of Vergence

Eye Movements

LAWRENCE E. MAYS

EYE MOVEMENT CONTROL subsystems have evolved to serve different functions. For example, the vestibulo-ocular reflex mechanisms help stabilize images on the retina in the face of head motion, and the saccadic subsystem allows for very rapid changes in the direction of gaze. Binocular vision requires that the two eyes be aligned on an object of interest to within about 15 minutes of arc. A vergence subsystem has evolved to achieve this goal.

Vergence commands are those that rotate the two eyes simultaneously in the opposite direction. They are distinguished from *versional* commands, such as saccades and smooth pursuit, where the eyes move in the same direction. Often, the terms *disjunctive* and *conjugate* are used to refer to vergence and versional movements, respectively. Some authors (Ono, 1983) use *version* and *vergence* to refer to the underlying mechanisms, while using *disjunctive* and *conjugate* to refer to the actual eye movements. Vergence movements may be horizontal, vertical, or torsional (i.e., rotation around the line of sight). Vertical and torsional vergence are small, generally reflexive eye movements, and while they are important for aligning the two eyes upon a target, relatively little is known about these types of movements (Kertesz, 1983). Horizontal vergence movements can be reflexive or voluntary and are needed when gaze is shifted between targets at differing distances from the observer. *Convergence* refers to lines of sight moving toward each other; *divergence* to the reverse. Unless stated otherwise, *vergence* as used here will refer to *horizontal* vergence movements. The control of horizontal vergence movements by the extraocular motoneurons and their premotor inputs will be reviewed.

Horizontal vergence is part of what has been called the *near triad* or *near response* (Myers and Stark, 1990). The other components of the near response are pupillary constriction (*miosis*) and *accommodation* of the crystalline lens, which changes the focal length of the eye. The miosis associated with convergence is somewhat questionable (Stakenburg, 1991), but the relationship between accommodation and convergence is quite robust. Indeed, accommodation of the eye, as when switching from a far to a near target, invariably induces convergence, even if the target is viewed monocularly. This linkage is termed *accommodative convergence* and is measured clinically as the *accommodative convergence/*

accommodation (AC/A) ratio. Moreover, convergence of the eyes induces accommodation, and this effect, termed *convergence accommodation*, is equally robust. The strength of this relationship is the CA/C (convergence accommodation/convergence) ratio. Considering the linkage between accommodation and vergence, it may not be surprising that the premotor neurons that control vergence appear to control accommodation as well.

Hering (1868) observed that the two eyes act as if yoked, that is, they move either the same amplitude in the same direction (version) or the same amplitude in the opposite direction (vergence). *Hering's Law of Equal Innervation* implies that all eye movements should be generated by a linear combination of largely independent versional (conjugate) commands and vergence (disconjugate) commands. In this view, conjugate commands operate on a *cyclopean eye*, an imaginary eye located between the two actual eyes. Many, but not all, studies of vergence control have used symmetrical vergence movements, in which the subject looks between targets at different distances aligned with the cyclopean eye in order to eliminate versional demands. An alternative view to Hering's Law states that the brain has independent control of each eye. This has been debated for over a century, and the debate continues (Enright, 1984; Zhou and King, 1998). The focus is on how to interpret what appear to be unequal saccades in the two eyes when vergence movements are combined with saccades.

Finally, considerable attention has been directed to the analysis of higher-order brain mechanisms for vergence control. Recent evidence suggests roles for the parietal cortex (Gnadt and Mays, 1995), frontal eye fields (Gamlin and Yoon, 2000), and superior colliculus (Chaturvedi and Van Gisbergen, 1999). Since these areas are involved in other types of eye movements, they may help coordinate vergence movements with saccades or perhaps smooth pursuit.

Extraocular motoneurons

Medial and lateral rectus muscles, which are innervated by motoneurons in the oculomotor and abducens nuclei, respectively, are primarily responsible for convergence and divergence. Figure 95.1 is a schematic diagram of these

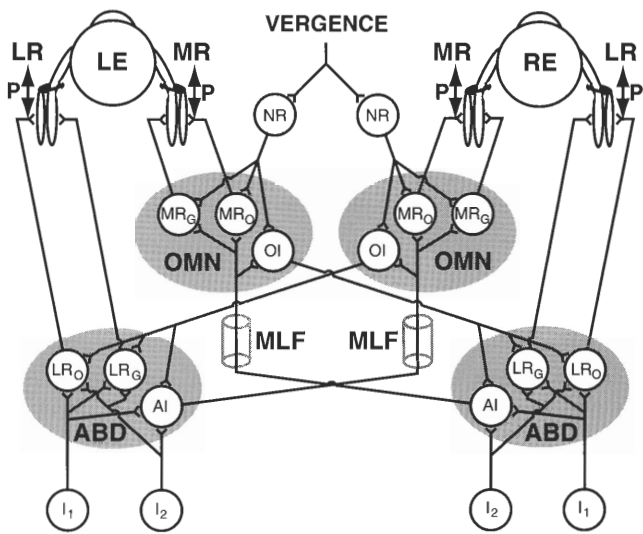


FIGURE 95.1. Schematic representation of horizontal oculomotor elements. Shaded ellipses indicate the oculomotor (OMN) and abducens (ABD) nuclei. The global layers of medial and lateral muscles are shown as inserting on the left (LE) and right eyes (RE). These layers are innervated by the subset of medial rectus (MR_G) and lateral rectus (LR_G) motoneurons. The orbital layers of these muscles are shown as inserting on muscle pulleys (P) and are innervated by the orbital subset of motoneurons (MR_O and LR_O). These MR_O and LR_O motoneurons appear to be responsible for moving the pulleys along an anterior-posterior axis (arrows). Abducens internuclear (AI) neurons are located in the abducens nucleus and send axons via the medial longitudinal fasciculus (MLF) to provide excitatory innervation to MR motoneurons and presumably oculomotor internuclear (OI) neurons as well. Many of the OI neurons are thought to project back to the ABD nucleus. Near response (NR) cells, which have a signal related to vergence and accommodation, appear to provide the needed vergence signal to MR motoneurons and probably provide the same signal to OI neurons. Two additional inputs (I_1 and I_2) are shown for ABD neurons. Hering's Law implies that I_1 and I_2 should be conjugate and vergence inputs, but recent work (Zhou and King, 1998) suggests that I_1 and I_2 are monocular ipsilateral and contralateral eye movement inputs.

motoneurons, as well as some of the premotor inputs to them. Extraocular motoneurons show a burst-tonic pattern of activity for saccades and have a linear relationship between firing rate and eye position (Robinson, 1970) for steady fixation.

NEURONS IN THE OCULOMOTOR NUCLEUS Two studies (Gamlin and Mays, 1992; Mays and Porter, 1984) showed that nearly all putative medial rectus (MR^*) motoneurons increased their activity for symmetrical convergence. This observation refuted earlier speculation (Alpern and Wolter, 1956) that a distinct subset of motoneurons was uniquely responsible for vergence movements. The comparison between the slope of the tonic firing rate-to-position relationship of a motoneuron for conjugate eye movements (versional gain) and that for purely symmetrical convergence

movements (vergence gain) is of particular interest. Figure 95.2 illustrates this comparison for a sample of horizontal burst-tonic neurons in the medial rectus subdivisions of the oculomotor nucleus. Overall, the mean vergence gain of MR^* motoneurons was essentially equal to that for changes in conjugate horizontal eye position, although the range of gains was much larger for convergence. Indeed, as Figure 95.2 shows, there is a very poor correlation between vergence gain and versional gain. If each motoneuron behaved in the same way for conjugate adduction as for convergence adduction, then all of the filled points in Figure 95.2 would fall along the line labeled "Ipsi eye." About 10% of MR motoneurons show little or no change in activity for convergence (points near the "Version only" line in Fig. 95.2), and another 10% have extremely high gains for vergence when compared to their versional gains. These recording studies may well have included some oculomotor internuclear (OI) neurons, which are located within the medial rectus subdivisions of the oculomotor nucleus but are not motoneurons (Fig. 95.1). An analysis of OIs (Clendaniel and Mays, 1994), identified by antidromic stimulation from the contralateral abducens nucleus, revealed activity profiles for versional and vergence eye movements which largely overlapped those of the larger sample of MR^* motoneurons (Fig. 95.2). One possible difference is that none of the OI neurons had the very high vergence gains seen in some MR^* cells, but this difference may be due to the very small sample of identified OIs. Interestingly, the activity of the OIs matched the activity of MR^* motoneurons for both version and vergence, even though the OIs projected to the contralateral abducens nucleus. If OIs conveyed useful information about vergence movements to the contralateral abducens, one would expect these cells to be aligned with the "Contra eye" line in Figure 95.2, which is not the case. This indicates that the OIs coordinate versional movements and not vergence.

NEURONS IN THE ABDUCENS NUCLEUS The vast majority of abducens neurons decrease their activity for convergence (Gamlin et al., 1989a; Maxwell, 1991; Mays and Porter, 1984). Figure 95.3 shows the vergence and versional gains of abducens neurons and of horizontal burst-tonic fibers in the medial longitudinal fasciculus (MLF). The latter are presumed to be axons of abducens internuclear neurons (AIs), which have somata in the abducens nucleus and project, via the MLF, to provide excitatory input to medial rectus motoneurons (Steiger and Büttner-Ennever, 1979). The filled symbols in Figure 95.3 show data from abducens neurons that presumably represent both lateral rectus motoneurons and AIs. Open circles show data from antidromically identified AI neurons. Cells that exhibit the same behavior for versional and vergence abduction would fall along the "Ipsi eye" line, those that change their activity

Oculomotor

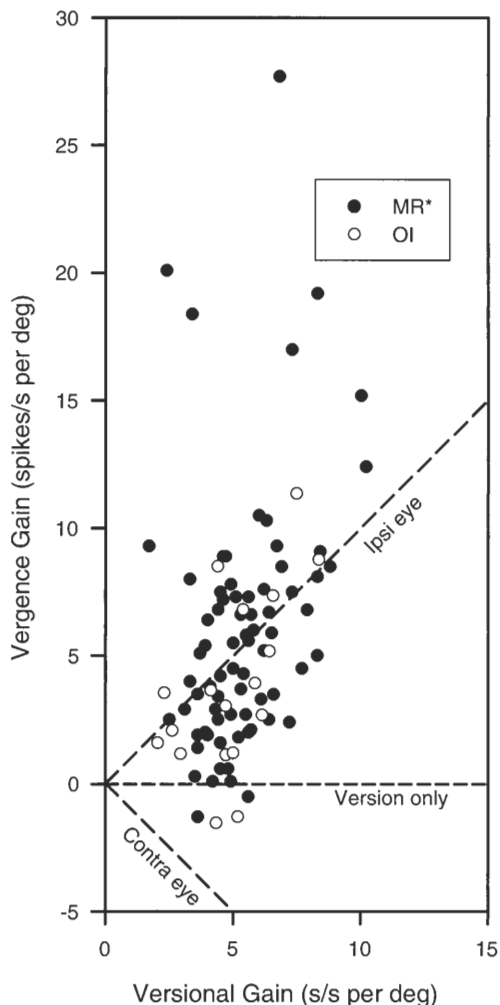


FIGURE 95.2. Distributions of static vergence and versional gains for neurons in the oculomotor nucleus displaying a burst-tonic firing pattern for conjugate adduction. Data are from Gamlin and Mays (1992). *Vergence gain* refers to the change in firing rate for each degree of adduction of the eye during symmetrical vergence movements. *Version gain* refers to the change in firing rate for each degree of adduction during conjugate saccades between distant targets. Positive values indicate increased activity for adduction. Open circles indicate oculomotor internuclear (OI) neurons, identified by antidromic stimulation from the contralateral abducens nucleus. Closed circles indicate cells with activity consistent with that of medial rectus (MR*) motoneurons but not positively identified as such. Data points falling along the dashed line labeled "Version only" represent cells that did not show any change in activity for symmetrical vergence movements. Data points on the "Ipsi eye" line showed the same change in activity for conjugate adduction as for symmetrical convergence. Any data points associated with the "Contra eye" line would have shown an increase in activity for conjugate adduction but a decrease for convergence, a pattern consistent with the innervation pattern for the contralateral eye. The overall activity pattern of OI neurons was very similar to that of putative MR* motoneurons. OI neurons did not have a Contra eye activity pattern, even though they project to the contralateral abducens nucleus. This suggests that OI neurons are used to coordinate horizontal conjugate movements and not vergence.

only for version would coincide with the "Version only" line, and those that fall along the "Contra eye" line would behave like contralateral MR motoneurons. Two important observations can be drawn from Figure 95.3. The first is that AIs (including MLF fibers) show the same pattern of responses as the overall population of abducens neurons, which presumably includes many lateral rectus (LR) motoneurons. The conclusion is that most LR motoneurons and AIs decrease their firing rate for convergence as well as for versional adduction. This is a critical observation since AIs provide powerful excitatory input to contralateral MR motoneurons. Since AIs decrease their activity for convergence, this means that they send an *inappropriate* signal to MR motoneurons during vergence movements. This implies that the AIs, like the OIs, coordinate conjugate horizontal eye movements and not vergence movements. The second observation is that, on average, abducens neurons do not reduce their firing rate as much for vergence adduction as for versional adduction. Indeed, most neurons in Figure 95.3 fall below the "Ipsi eye" line, which indicates equal firing rate change for version and vergence. This would suggest some degree of co-contraction of MR and LR muscles during convergence. However, recent measurements of LR and MR forces during convergence show no evidence of co-contraction (Miller et al., 2002). One possible reason for this apparent contradiction between muscle force measurements and motoneuron activity is that not all subsets of motor units develop equivalent forces for a given firing rate. Motoneurons responsible for larger decreases in muscle force during convergence may have been undersampled. Other explanations may involve the role of the trochlear motoneurons and muscle pulleys.

NEURONS IN THE TROCHLEAR NUCLEUS Although LR and MR muscles are primarily responsible for vergence eye movements, there is a well-known excyclotorsion of the eyes associated with convergence (Allen and Carter, 1967). The magnitude of this torsion depends on elevation of the eyes as well as the vergence angle, with greater excyclotorsion seen with ocular depression. A study of trochlear motoneurons (Mays et al., 1991) showed a systematic decrease in activity associated with convergence that was far larger than that expected from the values associated with conjugate abduction of the innervated eye. Moreover, the magnitude of the decrease in firing rate increased with ocular depression. These findings are consistent with the behavioral observation of excyclotorsion with convergence and with the lateral tilt of Listing's plane during convergence (van Rijn and Van der Berg, 1993). The decreased superior oblique tension could aid adduction during convergence (Mays et al., 1991), but a recent analysis (Miller et al., 2002) of all muscle forces indicates that this cannot explain the discrepancy between the motoneuron and muscle force data.

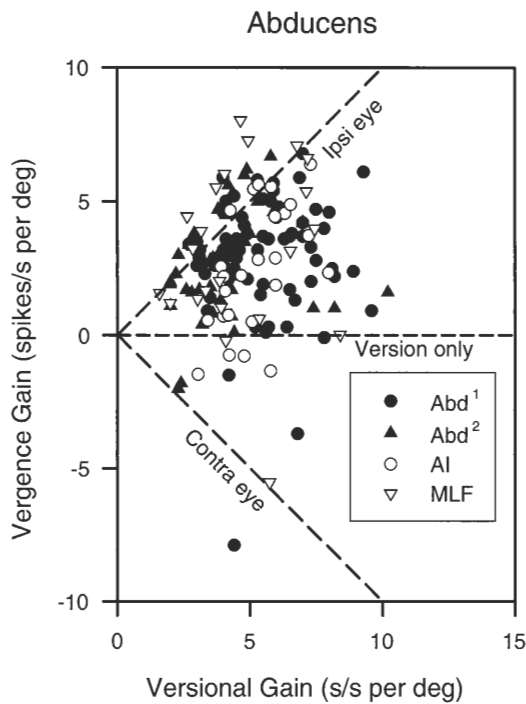


FIGURE 95.3. Distributions of static vergence and versional gains for neurons in the abducens nucleus displaying a burst-tonic firing pattern for conjugate abduction. *Vergence gain* refers to the change in firing rate for each degree of abduction of the eye for symmetrical vergence movements. *Version gain* refers to the change in firing rate for each degree of abduction during conjugate saccades between distant targets. Positive values indicate increased activity for abduction. Closed circles and triangles indicate cells with activity consistent with that of lateral rectus (LR) motoneurons but not positively identified as such. The closed circles (Abd^1), which are from Mays and Porter (1984) and Gamlin et al. (1989a), largely overlap the closed triangles (Abd^2) that were recorded by Maxwell (1991). Open circles indicate abducens internuclear (AI) neurons identified by antidromic stimulation of the medial longitudinal fasciculus (MLF) between the oculomotor and abducens nuclei. Open triangles are horizontal burst-tonic fibers recorded from the MLF, which are presumably axons of AI neurons. Data points falling along the dashed line labeled “Version only” represent cells that did not show any change in activity for symmetrical vergence movements. Data points on the “Ipsi eye” line showed the same change in activity for conjugate abduction as for symmetrical divergence. Most abducens neurons fell between the “Ipsi eye” and “Version only” lines, indicating that most decreased their activity for convergence and conjugate adduction, although the decrease for convergence was somewhat less. Any data points associated with the “Contra eye” line would have shown a decrease in activity for conjugate adduction but an increase for convergence, a pattern consistent with the innervation pattern for the contralateral eye. The overall activity pattern of AI neurons was very similar to that of the overall population of abducens neurons, which presumably included many LR motoneurons. Thus, most AI neurons decreased their firing rate for convergence, even though they project to the contralateral medial rectus (MR) motoneurons. This indicates that AI neurons send appropriate signals to the MR motoneurons to coordinate horizontal conjugate movements, but they do not provide the appropriate signals for vergence.

MUSCLE PULLEYS Recent evidence has shown that the effective origin of some eye muscles is altered by passing through slings or pulleys associated with Tenon’s capsule (Demer et al., 1995). These pulleys are shown schematically in Figure 95.1 as rings labeled “P.” It has been hypothesized that these pulleys provide a mechanical means for the eyes to obey Listing’s Law. Indeed, it appears that the LR pulleys are moved posteriorly during convergence, while the MR pulleys shift anteriorly in such a way as to produce the lateral tilt of Listing’s plane (Clark et al., 2000). Recent work (Demer et al., 2000) indicates that the orbital fiber layers of the LR and MR muscles insert on muscle pulleys and not on the globe itself. This implies that the activity of the motoneurons innervating orbital fibers in the pulley muscles (LR_O and MR_O in Fig. 95.1) may have very different activity patterns than the motoneurons innervating the global muscle fibers (LR_G and MR_G). Thus, the discrepancy between the LR motoneuron data and the absence of co-contraction may be due to recording a mixture of unidentified LR_O and LR_G motoneurons. To date, it has not been possible to distinguish between these motoneuron types with single-unit recording alone. The added biomechanical complexity of movable muscle pulleys makes it difficult to estimate muscle forces indirectly during convergence by observing the motoneuron firing rate from a combined motoneuron pool.

Premotor commands

NEAR RESPONSE CELLS AIs are a primary input to MR motoneurons for versional eye movements but not for vergence movements. This is implied by recording studies (Gamlin et al., 1989a) and convincingly demonstrated by clinical and experimental lesion studies (Gamlin et al., 1989b). Damage to the MLF, which carries AI axons, causes the clinical syndrome of internuclear ophthalmoplegia (Cogan, 1970), in which conjugate adduction is weakened or lost but convergence is preserved. This indicates that the MR motoneurons receive their vergence input from another source. Several studies (Judge and Cumming, 1986; Mays, 1984; Zhang et al., 1992) have conclusively demonstrated the presence of *near response* (“NR” in Fig. 95.1) cells in the midbrain reticular formation, just dorsal or lateral to the oculomotor nucleus, which carry signals related to vergence and accommodation but not version. Figure 95.4 shows the firing pattern of a near response cell for a symmetrical convergence movement. Most near response cells increase their activity for convergence (convergence cells). A smaller number of intermixed cells show the opposite response (divergence cells). For both types of cells, there is a nearly linear relationship between tonic firing rate and vergence angle and ocular accommodation. Many near response cells, including the one shown in Figure 95.4, also have a phasic

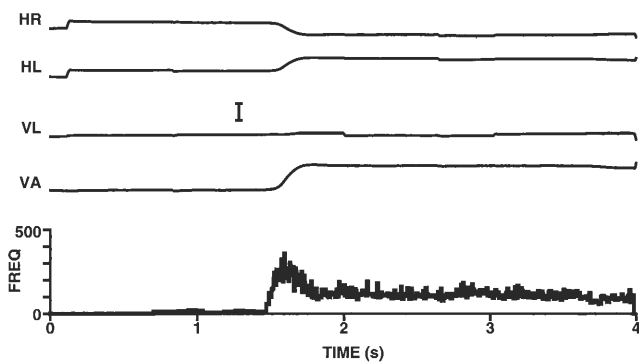


FIGURE 95.4. Activity pattern of a midbrain near response cell for symmetrical convergence. HR, horizontal right eye position; HL, horizontal left eye position; VL, vertical left eye position; VA, vergence angle, which is HL-HR. The firing rate is displayed as an instantaneous frequency histogram in spikes per second, which is the reciprocal of interspike interval. This neuron shows a linear tonic increase in activity for increasing convergence as well as a phasic increase related to convergence velocity. There is no change in firing rate for changes in conjugate eye position (not shown). Calibration bar = 5 degrees.

component to their activity that is related to vergence velocity. Some cells have *only* this phasic component for convergence (convergence burst cells) or divergence (divergence burst cells). For both types of burst cells, there is a nearly linear relationship between the number of spikes in the burst and the size of the vergence movement (Mays et al., 1986). Interestingly, this suggests that the vergence system, like the conjugate eye movement control systems, may be based on velocity commands and incorporates a vergence integrator to produce vergence position. Moreover, most MR motoneurons have both vergence position and vergence velocity signals (Gamlin and Mays, 1992). It has been possible to activate near response cells antidromically from the MR subdivisions of the ipsilateral oculomotor nucleus (Zhang et al., 1992). Based on the signals carried by these near response cells and the stimulation studies (Zhang et al., 1992), it seems very likely that the midbrain near response cells provide the needed vergence signals to the MR motoneurons.

Although the divergence and divergence burst cells have the signals needed by LR motoneurons, it has not yet been possible to determine if they project to the abducens nucleus. The most straightforward interpretation of Hering's Law would presume that conjugate (i.e., cyclopean) eye movement commands are provided to the abducens nucleus by one input (e.g., I_1 in Fig. 95.1), while a near response command, with the appropriate sign, is provided by a second input (I_2 in Fig. 95.1). This is in addition to the known near response input to MR motoneurons.

VERGENCE-ACCOMMODATION LINKAGE In order to understand the signals carried by the near response cells, the rela-

tionship between vergence and ocular accommodation has to be taken into account (Hung and Semmlow, 1980). Disparity-driven vergence can be considered as being under the control of a negative feedback servomechanism (Fig. 95.5). Referring to the top half of Figure 95.5, target distance determines convergence demand. The difference between the convergence demand and the convergence response is binocular disparity, which is the input to the vergence controller. The output of this controller goes eventually to the extraocular muscles (EOMs) to produce the convergence response. The goal of the vergence controller is to reduce disparity to an acceptably low level. A similar servomechanism is presumed to exist for the minimization of blur by an accommodation controller (lower half of Fig. 95.5). There is cross-coupling between these two control systems. In the absence of disparity, the accommodation system induces convergence with increases in accommodation. Similarly, increases in disparity-driven convergence result in increased accommodation. In normal viewing conditions, the two control systems function in a synergistic manner to provide the (covariant) appropriate amounts of accommodation and vergence.

An obvious question is whether the activity of midbrain near response cells (such as the one shown in Fig. 95.4) is related to accommodation or vergence. In terms of the model in Figure 95.5, a vergence-related near response cell would be located at the upper summing point (the small dashed ellipse labeled "VNR"), while an accommodation-related near response cell would be located at the lower summing point (the small dashed ellipse labeled "ANR"). For this analysis, it is necessary to dissociate the accommodative from the convergence responses. This can be done by attempting to vary accommodation while holding convergence constant or by varying convergence while holding accommodation constant. Although the two control systems are tightly coupled, some degree of dissociation of responses is possible. An early analysis of the activity of near response cells indicated that while a few cells could be classified as related to accommodation only, and another group appeared to be related to convergence only, the majority of near response cells were related to both (Judge and Cumming, 1986). A subsequent study of near response cells, including some that were activated by antidromic stimulation of the oculomotor nucleus and therefore in control of the vergence angle (Zhang et al., 1992), provided a model of how vergence (VNR) and accommodation (ANR) near response cells could be related both to accommodation and vergence.

Figure 95.6 shows the vergence and accommodation gains of 72 near response cells from the study by Zhang et al. (1992). Near response cells antidromically activated from the ipsilateral MR subdivisions of the oculomotor nucleus are shown as open circles; unidentified near response cells are

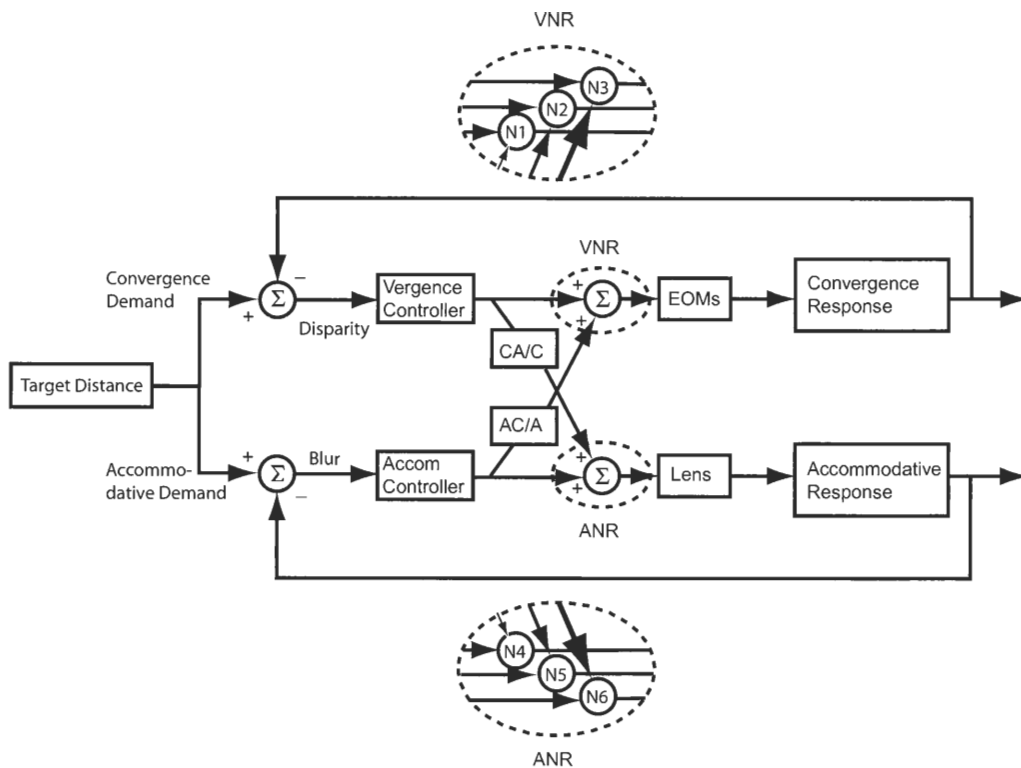


FIGURE 95.5. Dual interaction model of accommodation and vergence. Vergence and accommodation are controlled by their own negative feedback loops. In addition, part of the output of the accommodation controller is sent to the vergence subsystem. The gain of this cross-link is the AC/A ratio, and vergence near response (VNR) cells carry the summed signals. Part of the output of the vergence controller, with a gain corresponding to the CA/C ratio, is sent to the accommodation subsystem. The steady-state outputs of the accommodation and vergence controllers, and that of the cross-link components, can be calculated for any combina-

tion of convergence and accommodative demands as long as the CA/C and AC/A ratios are known. Accommodation near response (ANR) cells signal the sum of the output of the accommodation controller and the convergence accommodation signal. The large dashed ellipses represent a large number of near response cells, which receive direct and cross-link signals with different weights. The behavior of all recorded near response (N1 to N6) cells can be explained by assuming that different near response cells vary in the relative weights of their direct and cross-link inputs. EOMs, extraocular muscles.

shown as filled circles. The accommodation gain of a cell is the estimated change in firing rate for each diopter of accommodation if the vergence angle is held constant. The vergence gain is the estimated change in firing rate for each meter angle of convergence, if accommodation is held constant. The meter angle is a unit of angular measure that is comparable to the diopter (i.e., 1 M.A. is the angle between the eyes when viewing a target at 1 m). For the macaques used in this study, 1 M.A. is approximately 1.5 degrees. Any near response cell with activity related only to vergence angle, regardless of accommodation, would fall along the horizontal dashed line marked "Vergence Cell (N2)." Cells related exclusively to accommodation would fall along the vertical line marked "Accommodation Cell (N5)." Figure 95.6 shows that the majority of cells, whether identified as projecting to the oculomotor nucleus or not, are not uniquely related to accommodation or vergence alone but are related to both.

vergence near cells at the summing junction projecting to the oculomotor plant (dotted ellipse labeled "VNR") have exclusive control of the vergence angle. Similarly, the accommodation near cells at the summing junction projecting to the lens (dotted ellipse labeled "ANR") have exclusive control of the accommodation. Furthermore, there is no mixing of the outputs, implying that these signals are not shared between the extraoculomotor muscles and the ciliary muscle. The critical point associated with the results illustrated in Figure 95.6 is that both groups receive inputs from both the vergence and accommodation controllers, directly or through the cross-links. Consider the behavior of the model if one attempts to measure the accommodation gain of one of those cells by maintaining a constant level of convergence demand while increasing accommodation demand. Increasing accommodation demand will, accordingly, increase the accommodation level of the subject through the direct link between the accommodative controller and the accommodation near cells. At the same time, the increased accommodative signal will be sent to the vergence near cells

Near Response Cells

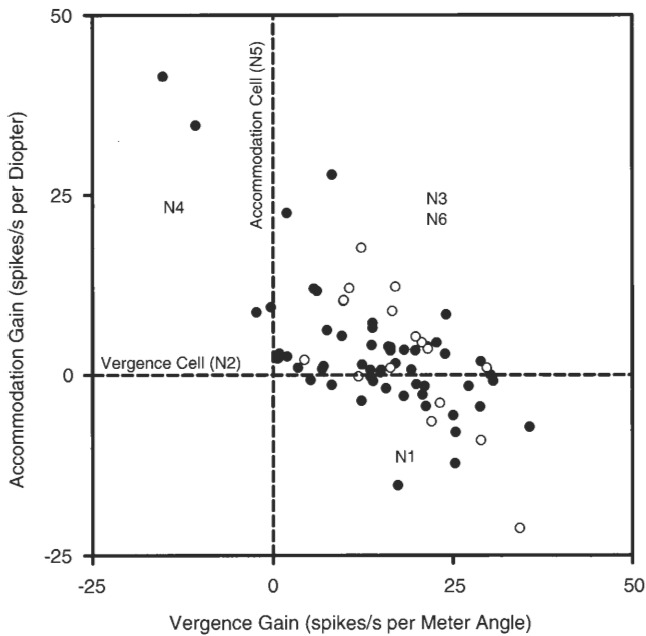


FIGURE 95.6. Relationship between vergence gain and accommodation gain for 72 near response cells. Data are from Zhang et al. (1992). Open circles represent a subset of these cells which were antidromically activated from the ipsilateral oculomotor nucleus and are presumed to be vergence near response (VNR) cells (see Fig. 95.5). *Accommodation gain* refers to the change in firing rate for each diopter of accommodation if the vergence angle remains constant. *Vergence gain* refers to the change in firing rate for each meter angle of convergence if accommodation remains constant. Note that, unlike Figures 95.2 and 95.3, vergence gain is calculated for total vergence angle in meter angles, which are comparable to diopters. Near response cells that have an accommodation gain of zero, and so have activity related exclusively to vergence angle, fall along the horizontal dashed line (Vergence Cell) and correspond to the vergence near response cells represented by N2 in Figure 95.5. Near response cells with activity related exclusively to accommodation (i.e., a vergence gain of zero) fall along the vertical dashed line and are represented in Figure 95.5 as N5 cells. Near response cells with a positive accommodation and vergence gain increase their activity for increases in either accommodation or convergence and are located in the upper right quadrant (N3 and N6 cells in Fig. 95.5). Near response cells with a negative accommodation gain and a positive vergence gain are located in the lower right quadrant. These cells *decrease* their activity with *increases* in accommodation, even though they otherwise increase their activity when accommodative and vergence demands increase appropriately (i.e., normal viewing conditions). This paradoxical behavior is due to the balance of direct and cross-link inputs as shown for N1 in Figure 95.5. Similarly, the cells in the upper left quadrant of Figure 95.6 have negative vergence gains, and so will decrease their activity for convergence if accommodation is held constant. These cells are represented by N4 in Figure 95.5.

through the AC/A cross-link to generate a covarying vergence change. This strategy is appropriate for what is normally needed in a natural environment, where vergence and accommodation are geometrically linked. However, in the situation where the vergence demand is left artificially unchanged, increasing accommodation will lead to over-convergence. This (negative) disparity error will engage the (di)vergence controller to reduce the vergence level of the subject to compensate for the unneeded vergence activation through the AC/A cross-link. This correction will also affect the accommodation level through the CA/C cross-link with additional (erroneous) changes in the accommodation level, and so on, but after a transitory period the subject will reach a steady-state condition. A similar sequence of events, starting with an increase in vergence demand, occurs when maintaining a constant level of accommodation demand while increasing vergence demand. How does this process affect the (steady-state) vergence and accommodation gains of a near response cell?

When the new steady state is reached, the vergence controller and the accommodation controller will have their output levels adjusted in such a way as to have the vergence and the accommodation levels matching the visual (dissociated) requirements in terms of vergence and accommodation. These adjustments at the controller level depend on the global AC/A and the CA/C ratios of the subject, but the important issue here is that these corrections are proportional to the variation imposed on the visual stimulus (i.e., the change in vergence demand for a fixed accommodation demand and vice versa). For example, keeping the vergence demand constant, larger changes in accommodation demands require larger changes in the output of the accommodation controller and proportional, but with a fixed ratio, negative changes in the output of the vergence controller to maintain an unchanged vergence level. The accommodative and vergence gains of each cell are determined by the relative amount of signal reaching the cell from the direct and cross-link inputs. These ratios will be determined by the global ratios of the subject, as well as by the individual weights of the direct and cross-link inputs to the cell. Depending on the resulting overall weights of the cell, we have three typical cases: (1) the ratio between the signal coming from the direct link and the cross-link is greater than 1; (2) it is exactly 1; (3) it is less than 1.

A vergence near cell with a ratio of exactly 1 (N2 in Fig. 95.5) will always receive equal and opposite signals from the direct and cross-link inputs during changes in accommodation only. The cell will appear insensitive to accommodation changes if they are not accompanied by vergence changes and so would be classified as a pure vergence cell. A cell with a ratio greater than 1 (i.e., a stronger direct link) will, under the same conditions, have a negative accommodation gain. This is because the negative direct corrective signal from the

vergence controller overcomes the positive accommodation signal from the cross-link (N1 in Fig. 95.5). A cell with a ratio less than 1 (i.e., stronger cross-link) will, in the same conditions, have a positive accommodation gain. The positive accommodation signal from the cross-link will overcome the negative direct corrective signal from the vergence controller (N3 in Fig. 95.5). The remarkable result is that all of these cells are, in terms of output, vergence cells, but depending on their weights, they can behave, at least partially, as “accommodation-related” cells. The same logic applies to the accommodation near cells (N5, N4, and N6, respectively) during changes in vergence with accommodation held constant, with, as a consequence, more or less “vergence-related” behavior. The overall schema does not change for vergence near cells during vergence changes with fixed accommodation demand or for accommodation near cells during accommodation changes with fixed vergence demand. The global AC/A and CA/C ratios of the subject are normally less than 1, when measured in comparable units (i.e., diopters and meter angles).

These theoretical considerations result in predictions that match the data in Figure 95.6 very closely. The two cells in the upper left quadrant of Figure 95.6 were not antidromically activated from the oculomotor nucleus. This is consistent with the model, since the N4 type cells would have to be in the accommodation output path. Vergence near response cells represented by N3 would show a positive vergence gain and a positive accommodation gain, but so would cells represented by N6 in the accommodation output path. Using plausible values for the AC/A and CA/C ratios, no near response cells that increase their activity for covariant convergence and accommodation should be seen in the lower left quadrant of Figure 95.6 using dissociated stimuli. Indeed, no cells were found with a negative accommodation gain and a negative vergence gain using the dissociated stimuli. This analysis shows that a biologically plausible distribution of differing direct and cross-link inputs to near response cells can account for the wide variety of vergence and accommodation gains, including negative gain values.

Saccade-vergence interactions

UNEQUAL HORIZONTAL SACCADES Although the analysis of near response cells clearly demonstrates the presence of vergence-related signals, Hering’s Law suggests that we should also see premotor signals related exclusively to conjugate commands, that is, to movements of the cyclopean eye. Saccadic eye movements are assumed to be intrinsically conjugate. In other words, both eyes execute identical rotations of an amount related to the needs of the cyclopean eye. This assumption has been challenged by observations that horizontal saccades may be markedly unequal in amplitude if they are executed together with a vergence move-

ment. Figure 95.7A shows a smooth symmetrical convergence movement approximately 10 degrees in size made by a macaque. This movement was made between far and near targets aligned with the cyclopean eye and contained no saccades. The vergence velocity (VV) trace shows that the peak velocity of this movement was approximately 50 degrees. This is about an order of magnitude slower than the peak velocity of a conjugate saccade of similar size. Figure 95.7B shows a similar size convergence movement combined with a rightward saccade, indicated by an arrow. The rightward saccade made by the right eye appears to be two to three times smaller than the saccade made by the left eye. Careful analysis of saccades during vergence in both the human (Ono et al., 1978) and the macaque (Maxwell and King, 1992) has shown that the differences in saccade size between the two eyes cannot be attributed to the ongoing smooth vergence movement. That is, the difference in saccade size is larger than the one expected by the linear combination of the version and smooth vergence. This is more clearly shown by an inspection of the vergence velocity trace of Figure 95.7B, which shows an abrupt doubling of vergence velocity associated with the saccade. Hering’s Law would predict that the vergence velocity profile in Figure 95.7B would be the same as for smooth vergence in Figure 95.7A.

DO UNEQUAL SACCADES IMPLY MONOCULAR CONTROL?

Markedly unequal horizontal saccades during vergence have been interpreted by some investigators (Enright, 1992) as a clear violation of Hering’s Law. Enright (1984) and others (Dell’Osso, 1994; Zhou and King, 1998) have suggested that the control mechanisms for the two eyes may be intrinsically independent. In this view, although many eye movements are conjugate, the underlying circuitry allows for independent control of the two eyes for smooth pursuit eye movements (King and Zhou, 1995) and for saccades (Enright, 1984). Any difference in the monocular commands to the two eyes would generate changes in the vergence profile that are not associated with the vergence system proper. Zee and colleagues (1992) have suggested alternative eye movement models that can produce unequal saccades without invoking monocular control. The critical observation for these models is that vertical saccades can also cause vergence to be speeded. An example of this can be seen in Figure 95.7C, which shows a small (2.5 degree) downward saccade which occurs during a 10 degree convergence movement. An examination of the vergence velocity trace in Figure 95.7C shows that its peak is more than doubled by the occurrence of the saccade (i.e., compare to VV in Fig. 95.7A). This indicates that the speeding of vergence depends on the occurrence of a saccade in any direction rather than the generation of unequal *horizontal* saccades.

Zee et al. (1992) have evaluated several models of saccade-vergence interactions, where vertical saccades can

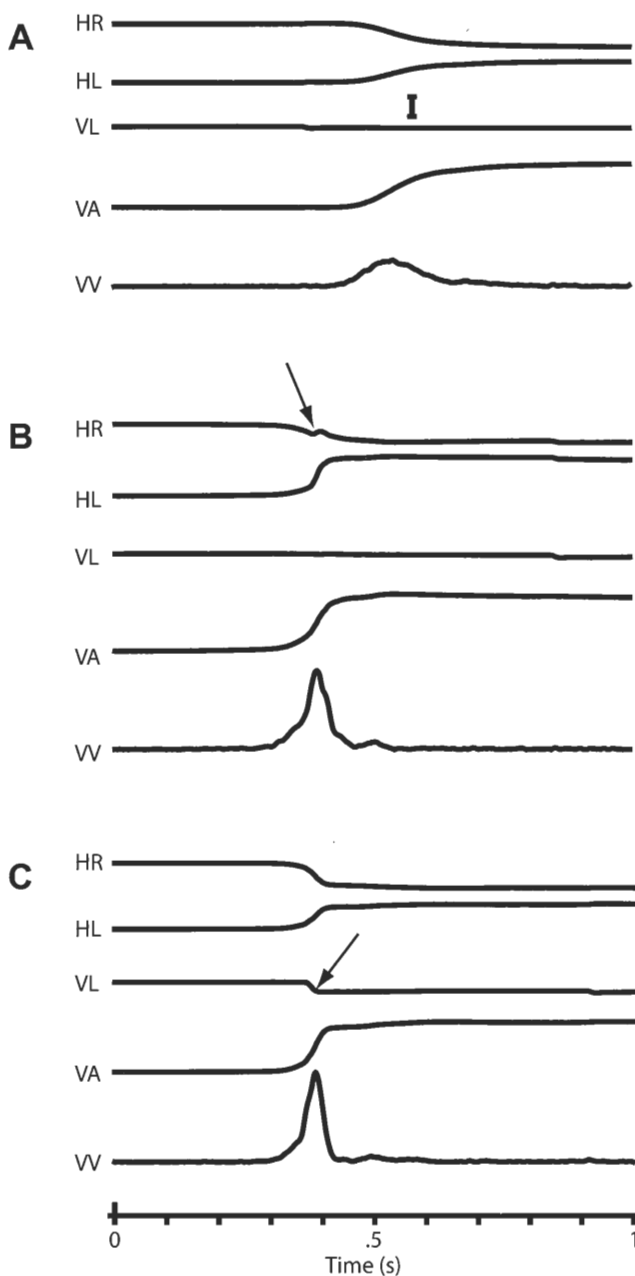


FIGURE 95.7. Saccade-vergence interactions. Convergence in the absence of a saccade (*A*), similar convergence with a horizontal (rightward) saccade (*B*), and similar convergence with a vertical (downward) saccade (*C*). The arrows in *B* and *C* indicate the occurrence of a saccade. The calibration bar corresponds to 5 degrees for eye position traces and 50 deg/sec for the vergence velocity (VV) trace. Eye position trace abbreviations are as in Figure 95.4. The occurrence of a saccade during the early phase of a vergence movement (either convergence or divergence) results in an immediate increase in vergence velocity, even if the saccade is purely vertical (*C*). This indicates that the mechanism by which vergence is speeded by a saccade does not depend on unequal horizontal saccadic rotations.

also speed vergence. Two related models, which are alternatives to the independent eye control hypothesis, allow for vergence-related neural activity to be gated by pontine omnipause neurons (OPNs) (Keller, 1974). Both models simulate saccade-vergence interactions reasonably well. One of these models, the OPN model, is consistent with two critical observations: (1) the enhancement of vergence velocity by vertical saccades (Enright, 1984; Zee et al., 1992), which could implicate the pontine OPNs (which are omnidirectional) in this interaction, and (2) the existence of midbrain vergence burst neurons which carry vergence velocity signals (Mays et al., 1986). These observations suggest that a vergence velocity signal could be modulated by saccade-related (i.e., OPN) activity.

The inputs to the OPN model are pure symmetric vergence and pure conjugate saccadic commands. Consider a convergence-saccade combination with a horizontal saccade that occurs near the beginning of the convergence. This situation typically produces markedly unequal horizontal saccades. In the absence of a saccade, a slow vergence command is relayed to convergence burst (CB) cells that are tonically, but weakly, inhibited by OPNs. Consequently, only slow vergence movements can occur in the absence of a saccade (Fig. 95.7*A*). The occurrence of a saccade is associated with the cessation of activity in the OPNs, which results in a release of the inhibition of the CB cells. The disinhibited CB cells produce an additional pulse of vergence activity that is processed through the vergence neural integrator, and the resulting position signal is combined with the vergence velocity signal at the CB-tonic cells. The output of these cells is added to the ongoing saccadic horizontal pulse and step commands communicated to the MR motoneurons by the AI neurons. The simple linear addition of these commands produces an accentuated pulse-step command for one eye and a diminished pulse-step command for the other eye, resulting in markedly unequal horizontal saccades in the two eyes (Fig. 95.7*B*). Since this depends on the omnidirectional OPN cells, saccades in all directions, including vertical saccades (Fig. 95.7*C*), will be equally effective in speeding vergence. Although this model requires more rigorous testing, it demonstrates that unequal horizontal saccades do not necessarily imply monocular saccadic control mechanisms for each eye.

Conjugate versus monocular commands

EXCITATORY BURST NEURONS The monocular control hypothesis suggested by Enright (1984) and the saccadic facilitation of vergence hypothesis described by Zee et al. (1992) imply very different ways of generating saccades and vergence eye movements. One way of resolving this issue would be to record premotor signals during these unequal horizontal saccades to determine if they are related to the

movement of the cyclopean eye (Hering's Law) or to the separate movements of the two eyes. This experiment has been reported by Zhou and King (1998), who recorded from putative excitatory burst neurons (EBNs), located in the pons near the abducens nucleus. EBNs project to the ipsilateral abducens nucleus and show a burst of activity that is related to the horizontal component of ipsilateral saccades. Specifically, the number of spikes in each burst is believed to be linearly proportional to the horizontal size of the saccade (Keller, 1974). Taking advantage of this relationship, Zhou and King counted the number of spikes recorded from EBNs during unequal-amplitude horizontal saccades. By comparing the number of spikes in the burst during unequal saccades with the number of spikes for conjugate saccades, Zhou and King determined if the burst was associated with the amplitude of the rotation of the ipsilateral eye, the contralateral eye, or the cyclopean eye. Although the activity of a few EBNs was associated with the cyclopean eye during unequal saccades, as expected by Hering's Law, the activity of the majority of EBNs was more closely associated with the rotation of either the ipsilateral or the contralateral eye.

OTHER MONOCULAR SIGNALS Zhou and King (1998) also reported that the majority of cells recorded in the nucleus prepositus hypoglossi, an area thought to produce horizontal eye position signals, were also monocular. McConville et al. (1994) recorded position-vestibular-pause cells in the vestibular nuclei of macaques during conjugate and vergence eye movements. They found that 18 out of 20 cells had monocular eye position signals.

HOW ARE MONOCULAR EYE COMMANDS USED? The results of Zhou and King are inconsistent with the idea that neurons in the abducens nucleus are provided with separate conjugate and vergence inputs, as required by Hering's Law. Instead, they strongly suggest that the inputs I_1 and I_2 in Figure 95.1 do not reflect conjugate and vergence inputs, but instead represent ipsilateral and contralateral eye commands. This new conjecture raises a puzzling question: how are these monocular commands used? A number of studies (Gamlin et al., 1989a; Maxwell, 1991; Mays and Porter, 1984), including data from Zhou and King, show that even if the inputs to the abducens nucleus represent monocular signals, the activity of the vast majority of abducens neurons is not monocularly coded. This can be seen in Figure 95.3. Abducens neurons with activity reflecting an ipsilateral monocular input would fall along the "Ipsi eye" dashed line, while those with activity related to the other eye would fall along the "Contra eye" line. While there are a number of cells with activity corresponding to a monocular ipsilateral eye input, there are very few with activity related to the contralateral eye. Indeed, most abducens neurons show an

activity pattern that is between the ipsi and contra eye lines. This indicates that if ipsilateral and contralateral eye movement signals are provided to neurons in the abducens nucleus, these signals are commingled and individual eye position information is lost on the abducens neurons. This finding is consistent with the AI and MLF recording data, as well as lesion studies (cited above), which demonstrate that neurons in the abducens nucleus do not provide an appropriate vergence signal to the MR motoneurons. Furthermore, monocular eye position and velocity signals do not appear to be used for the generation of vergence eye movements, at least via the abducens nucleus. This strongly implies that the vergence angle changes brought about by unequal horizontal saccades are not due to activity differences between abducens motoneurons and internuclear neurons.

It is possible that in primates these premotor monocular signals have lost their original function. From an evolutionary point of view, a fully developed vergence system with depth perception (stereopsis) is present only in primates. Primitive lateral-eye animals do not have a vergence system. In these animals, each eye is controlled independently; therefore, there is a need for appropriate monocular commands to be sent to each eye. This raises the possibility that the migration of the eyes from a lateral position to a frontal one with the development of an independent precise vergence system able to maintain the accurate binocular alignment needed by stereopsis was accompanied by the fusion of the original monocular signals into a single cyclopean structure. Disjunctive signals, generated independently by the vergence system, were simultaneously added to the motoneurons to allow precise disjunctive eye movements to be guided by disparity errors. These are also binocular from a sensory point of view. It should be noted that the precision required by the vergence system for stereopsis is much higher than that required by the versional systems (or the monocular ones in the evolutionarily primitive animals). This is even true in foveate animals, where the object of interest has to be projected over a small area of the retina for the best spatial resolution. Perhaps the inherent lack of precision achievable by a monocular arrangement pressed evolution toward a versional/vergence solution. The need for a positional vergence signal is also important in frontal-eye animals to estimate the viewing distance of the object of interest to program, accordingly, the gain of the vestibulo-ocular reflexes. For a review of this issue, see Miles (1995). An alternative possibility is that these monocular premotor signals were initially generated as versional signals, from which vergence signals were subtracted later on, perhaps to improve dynamic performance. At present, there is no way to distinguish between these alternatives.

CEREBELLUM AND PONTINE AREAS There is some evidence that the cerebellum is involved in the near response. Westheimer and Blair (1973) reported transient vergence deficits after cerebellectomy in primates. Zhang and Gamlin (1998) found cells in the posterior interposed nucleus of the cerebellum related to vergence and accommodation. All of these cells increased their activity for divergence and so were described as *far response* cells. Gamlin and Clarke (1995) reported cells related to either near or far responses in the medial zone of the nucleus reticularis tegmenti pontis (NRTP), a precerebellar nucleus. Although these cells were often found near cells with saccade-related activity, the vergence-related cells did not change their activity in association with saccades or conjugate pursuit. The NRTP has reciprocal connections with the midbrain area containing the near response cells that, in turn, project to the oculomotor nucleus (May et al., 1992). Moreover, the NRTP is an area that receives cortical inputs and also has reciprocal connections with the cerebellum. It may be an important link providing vergence and accommodation signals to both the cerebellum and the midbrain near response areas.

SUPERIOR COLLICULUS The superior colliculus (SC) has long been implicated in the initiation of saccades and, more recently, in the control of gaze saccades (Freedman and Sparks, 1997) (i.e., combined rapid movements of the head and eyes). In the head-fixed animal, stimulation of most of the SC induces stereotyped conjugate contralateral saccades (Robinson, 1972). Stimulation of the rostral pole of the SC, which can inhibit saccades (Munoz and Wurtz, 1993), also partially inhibits convergence (Chaturvedi and Van Gisbergen, 2000), and stimulation of more caudal areas of the SC perturbs both ongoing saccades and vergence. Many neurons in the SC produce a burst of activity before specific contralateral saccades, but there have been no published reports of SC neurons firing for vergence in the absence of saccades. Preliminary data from our laboratory indicate that many saccade-related SC burst neurons fire less vigorously for saccades during both convergence and divergence than for conjugate saccades. This decrease in activity may be related to the report that saccades executed during vergence may be slower and longer than saccades of similar size without vergence (Collewijn et al., 1995). While there are some indications that the SC may be involved in saccade-vergence interactions, the significance of these observations remains unclear.

FRONTAL EYE FIELD The frontal eye field (FEF) area in macaques is located in the region of the arcuate sulcus. FEF cells fire in response to visual stimuli and also in relation to

saccades to visual stimuli (Bruce and Goldberg, 1985). Some neurons in the floor and posterior bank of the arcuate sulcus also discharge for smooth pursuit eye movements (Gottlieb et al., 1994). Recently, Gamlin and Yoon (2000) reported finding vergence- and accommodation-related cells just anterior to the arcuate sulcus. Most cells increased their activity for convergence, but some far response cells were observed as well. The activity of these cells appeared to be closely related to motor output, although several cells were responsive to the visual stimulus eliciting the near response. A small minority of cells were modulated during versional eye movements as well as during vergence. Microstimulation of an area anterior to the arcuate sulcus resulted in accommodation and convergence. The FEF projects to the NRTP, to the SC, and to brainstem oculomotor areas (Leichnetz, 1981; Leichnetz et al., 1984), and so may provide vergence and accommodation commands to these areas, as well as pursuit and saccadic commands.

PARIETAL CORTEX Many neurons in parietal cortex show a complex relationship between their activity and saccades, smooth pursuit, and fixation. A substantial number of neurons in the lateral intraparietal sulcus (LIP) discharge for saccades. A majority of these saccade-related neurons also show a modulation in activity associated with the vergence component when a saccade is combined with vergence (Gnadt and Mays, 1995). It appears that many cells are tuned for gaze shifts in three-dimensional space. More recently, Gnadt and Beyer (1998) antidromically activated a subset of LIP neurons with three-dimensional movement fields from the SC. This suggests a way in which vergence information, as well as saccadic signals, could be sent to the SC.

OTHER CORTICAL AREAS A number of other cortical areas have neurons that could provide information about the distance of an object from the viewer. Some neurons in ventral intraparietal cortex (VIP) (Colby et al., 1993) discharge most vigorously for visual stimuli near the face. Others fired for visual stimuli moving toward the animal. Areas MT (middle temporal) and MST (medial superior temporal) in the superior temporal sulcus have neurons that encode disparity and so may be important for tracking objects in three-dimensional space (Kawano et al., 2000). Other visual cortical areas, such as V1, contain neurons sensitive to binocular stimulation. Some of these neurons are particularly sensitive to targets near the plane of fixation (tuned-zero neurons), while others respond best to targets closer to (near cells) or beyond (far cells) the plane of fixation (Poggio, 1995). In short, there are many cortical areas with signals that could be used to control vergence movement. Whether or not signals in a particular area are, in fact, used for this purpose is unknown.

Summary

The activity patterns of extraocular motoneurons during versional and vergence eye movements have been well characterized. The biomechanical complexity of the oculomotor plant, especially with the recent discovery of movable muscle pulleys, has made the task of relating motoneuron activity to muscle forces quite difficult, as Miller et al. (2002) have pointed out. A better assessment of the role of the muscle pulleys, and of the mechanical coupling between the orbital and global muscle layers, is needed to resolve the discrepancy between muscle force data and motoneuron activity for vergence movements. This should be accompanied by recordings from motoneurons identified as innervating global or orbital muscle fibers.

There has been significant progress in understanding premotor near response commands and the role of near response cells in coordinating accommodation and vergence. Surprisingly, the nature of the commands used for conjugate eye movements needs further clarification. Recent work indicates that these premotor commands may be monocular, but it appears that these "monocular" signals are commingled to construct what is essentially a conjugate (cyclopean) signal at the level of the motoneurons. The evolutionary history of eye movement circuits may provide an explanation of why such a scheme should exist.

The debate as to whether the premotor commands are monocular or represent a combination of cyclopean and vergence signals has often centered on the nature of saccade-vergence interactions. The observation of horizontal saccades of different amplitudes does not, in itself, indicate that the control of the saccades is inherently monocular. A better understanding of the mechanism by which vergence speed is increased during saccades is needed.

The route by which vergence commands are generated and sent to near response neurons is unknown. Recent studies of the NRTP, the cerebellar interposed nucleus, and the FEF suggest several possibilities, but the details need to be provided. Visual cortical areas have an embarrassingly large number of disparity- and spatial frequency (blur)-sensitive neurons, but no direct linkage between the activity of these cells and the near response has been demonstrated.

Acknowledgment

I thank Dr. Claudio Busettini for his helpful comments on the manuscript and for his assistance in preparing the figures.

REFERENCES

- Allen, M. J., and J. H. Carter, 1967. The torsion component of the near reflex. A photographic study of the non-moving eye in unilateral convergence, *Am. J. Optom. Arch. Am. Acad. Optom.*, 44:343–349.
- Alpern, M., and J. R. Wolter, 1956. The relation of horizontal saccadic and vergence movements, *AMA Arch. Ophthalmol.*, 56:685–690.
- Bruce, C. J., and M. E. Goldberg, 1985. Primate frontal eye fields. I. Single neurons discharging before saccades, *J. Neurophysiol.*, 53:603–635.
- Chaturvedi, V., and J. A. M. Van Gisbergen, 1999. Perturbation of combined saccade-vergence movements by microstimulation in monkey superior colliculus, *J. Neurophysiol.*, 81:2279–2296.
- Chaturvedi, V., and J. A. M. Van Gisbergen, 2000. Stimulation in the rostral pole of monkey superior colliculus: effects on vergence eye movements, *Exp. Brain Res.*, 132:72–78.
- Clark, R. A., J. M. Miller, and J. L. Demer, 2000. Three-dimensional location of human rectus pulleys by path inflections in secondary gaze positions, *Invest. Ophthalmol. Vis. Sci.*, 41:3787–3797.
- Clendaniel, R. A., and L. E. Mays, 1994. Characteristics of antidromically identified oculomotor internuclear neurons during vergence and versional eye movements, *J. Neurophysiol.*, 71:1111–1127.
- Cogan, D. G., 1970. Internuclear ophthalmoplegia, typical and atypical, *Arch. Ophthalmol.*, 84:583–589.
- Colby, C. L., J. R. Duhamel, and M. E. Goldberg, 1993. Ventral intraparietal area of the macaque: anatomic location and visual response properties, *J. Neurophysiol.*, 69:902–914.
- Collewijn, H., C. J. Erkelens, and R. M. Steinman, 1995. Voluntary binocular gaze-shifts in the plane of regard: dynamics of version and vergence, *Vis. Res.*, 35:3335–3358.
- Dell'Osso, L. F., 1994. Evidence suggesting individual ocular motor control of each eye (muscle), *J. Vest. Res.*, 4:335–345.
- Demer, J. L., J. M. Miller, V. Poukens, H. V. Vinters, and B. J. Glasgow, 1995. Evidence for fibromuscular pulleys of the recti extraocular muscles, *Invest. Ophthalmol. Vis. Sci.*, 36:1125–1136.
- Demer, J. L., S. Y. Oh, and V. Poukens, 2000. Evidence for active control of rectus extraocular muscle pulleys, *Invest. Ophthalmol. Vis. Sci.*, 41:1280–1290.
- Enright, J. T., 1984. Changes in vergence mediated by saccades, *J. Physiol.*, 350:9–31.
- Enright, J. T., 1992. The remarkable saccades of asymmetrical vergence, *Vis. Res.*, 32:2261–2276.
- Freedman, E. G., and D. L. Sparks, 1997. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys, *J. Neurophysiol.*, 77:2328–2348.
- Gamlin, P. D. R., and R. J. Clarke, 1995. Single-unit activity in the primate nucleus reticularis tegmenti pontis related to vergence and ocular accommodation, *J. Neurophysiol.*, 73:2115–2119.
- Gamlin, P. D. R., J. W. Gnadt, and L. E. Mays, 1989a. Abducens internuclear neurons carry an inappropriate signal for ocular convergence, *J. Neurophysiol.*, 62:70–81.
- Gamlin, P. D. R., J. W. Gnadt, and L. E. Mays, 1989b. Lidocaine-induced unilateral internuclear ophthalmoplegia: effects on convergence and conjugate eye movements, *J. Neurophysiol.*, 62:82–95.
- Gamlin, P. D. R., and L. E. Mays, 1992. Dynamic properties of medial rectus motoneurons during vergence eye movements, *J. Neurophysiol.*, 67:64–74.
- Gamlin, P. D. R., and K. Yoon, 2000. An area for vergence eye movement in primate frontal cortex, *Nature*, 407:1003–1007.

- Gnadt, J. W., and J. Beyer, 1998. Eye movements in depth: what does the monkey's parietal cortex tell the superior colliculus? *NeuroReport*, 9:233–238.
- Gnadt, J. W., and L. E. Mays., 1995. Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space, *J. Neurophysiol.*, 73:280–297.
- Gottlieb, J. P., M. G. Macavoy, and C. J. Bruce, 1994. Neural responses related to smooth-pursuit eye movements and their correspondence with electrically elicited smooth eye movements in the primate frontal eye field, *J. Neurophysiol.*, 72:1634–1653.
- Hering, E., 1868. *Die Lehre vom binocularen Sehen*, [The Theory of Binocular Vision (B. Bridgeman and L. Stark, trans.), New York: Plenum Press; Leipzig: W. Engelmann].
- Hung, G. K., and J. L. Semmlow, 1980. Static behavior of accommodation and vergence: computer simulation of an interactive dual-feedback system, *IEEE Trans. BME*, 27:439–447.
- Judge, S. J., and B. G. Cumming, 1986. Neurons in the monkey midbrain with activity related to vergence eye movement and accommodation, *J. Neurophysiol.*, 55:915–930.
- Kawano, K., Y. Inoue, A. Takemura, Y. Kodaka, and F. A. Miles, 2000. The role of MST neurons during ocular tracking in 3D space, in *Neuronal Processing of Optic Flow* (M. Lappe ed.), San Diego, CA: Academic Press, pp. 49–63.
- Keller, E. L., 1974. Participation of medial pontine reticular formation in eye movement generation in monkey, *J. Neurophysiol.*, 37:316–332.
- Kertesz, A. E., 1983. Vertical and cyclofusional disparity vergence, in *Vergence Eye Movements: Basic and Clinical Aspects* (C. M. Schor and K. J. Ciuffreda, eds.), Boston: Butterworths, pp. 317–348.
- King, W. M., and W. Zhou., 1995. Initiation of disjunctive smooth pursuit in monkeys: evidence that Hering's law of equal innervation is not obeyed by the smooth pursuit system, *Vis. Res.*, 35:3389–3400.
- Leichnetz, G. R., 1981. The prefrontal cortico-oculomotor trajectories in the monkey, *J. Neurol. Sci.*, 49:387–396.
- Leichnetz, G. R., D. J. Smith, and R. F. Spencer, 1984. Cortical projections to the paramedian tegmental and basilar pons in the monkey, *J. Comp. Neurol.*, 228:388–408.
- Maxwell, J. S., 1991. The interaction of saccades and vergence eye movements and the effect of vergence angle on the discharge rate of abducens neurons in monkeys. Unpublished dissertation, University of Rochester.
- Maxwell, J. S., and W. M. King, 1992. Dynamics and efficacy of saccade-facilitated vergence eye movements in monkeys, *J. Neurophysiol.*, 68:1248–1260.
- May, P. J., J. D. Porter, and P. D. R. Gamlin, 1992. Interconnections between the primate cerebellum and midbrain near-response regions, *J. Comp. Neurol.*, 315:98–116.
- Mays, L. E., 1984. Neural control of vergence eye movements: convergence and divergence neurons in mid-brain, *J. Neurophysiol.*, 51:1091–1108.
- Mays, L. E., and J. D. Porter. 1984. Neural control of vergence eye movements: activity of abducens and oculomotor neurons, *J. Neurophysiol.*, 52:743–761.
- Mays, L. E., J. D. Porter, P. D. R. Gamlin, and C. A. Tello, 1986. Neural control of vergence eye movements: neurons encoding vergence velocity, *J. Neurophysiol.*, 56:1007–1021.
- Mays, L. E., Y. Zhang, M. H. Thorstad, and P. D. R. Gamlin, 1991. Trochlear unit activity during ocular convergence, *J. Neurophysiol.*, 65:1484–1491.
- McConville, K., R. D. Tomlinson, W. M. King, G. Paige, and E. Q. Na, 1994. Eye position signals in the vestibular nuclei: consequences for models of integrator function, *J. Vest. Res.*, 4:391–400.
- Miles, F. A., 1995. The sensing of optic flow by the primate optokinetic system, in *Eye Movement Research: Mechanisms, Processes and Applications* (J. M. Findlay, R. W. Kentridge, and R. Walker, eds.), Amsterdam: Elsevier, pp. 47–62.
- Miller, J. M., C. J. Bockisch, and D. S. Pavlovski, 2002. Missing lateral rectus force and absence of medial rectus co-contraction in ocular convergence, *J. Neurophysiol.*, 87:2421–2433.
- Munoz, D. P., and R. H. Wurtz., 1993. Fixation cells in monkey superior colliculus. II. Reversible activation and deactivation, *J. Neurophysiol.*, 70:576–589.
- Myers, G. A., and L. Stark, 1990. Topology of the near response triad, *Ophthalmic. Physiol. Opt.*, 10:175–181.
- Ono, H., 1983. The combination of version and vergence, *Vergence Eye Movements: Basic and Clinical Aspects* (C. M. Schor and K. J. Ciuffreda, eds.), Boston: Butterworths, pp. 373–400.
- Ono, H., S. Nakamizo, and M. J. Steinbach, 1978. Nonadditivity of vergence and saccadic eye movement, *Vis. Res.*, 18:735–739.
- Poggio, G. E., 1995. Mechanisms of stereopsis in monkey visual cortex [review], *Cereb. Cortex*, 5:193–204.
- Robinson, D. A., 1970. Oculomotor unit behavior in the monkey, *J. Neurophysiol.*, 33:393–404.
- Robinson, D. A., 1972. Eye movements evoked by collicular stimulation in the alert monkey, *Vis. Res.*, 12:1795–1808.
- Stakenburg, M., 1991. Accommodation without pupillary constriction, *Vis. Res.*, 31:267–273.
- Steiger, H. J., and J. A. Büttner-Ennever, 1979. Oculomotor nucleus afferents in the monkey demonstrated with horseradish peroxidase, *Brain Res.*, 160:1–15.
- van Rijn, L. J., and A. V. Van der Berg, 1993. Binocular eye orientation during fixations: Listing's law extended to include eye vergence, *Vis. Res.*, 33:691–708.
- Westheimer, G., and S. M. Blair, 1973. Oculomotor defects in cerebellectomized monkeys, *Invest. Ophthalmol.*, 12:618–621.
- Zee, D. S., E. J. Fitzgibbon, and L. M. Optican, 1992. Saccade-vergence interactions in humans, *J. Neurophysiol.*, 68:1624–1641.
- Zhang, H. and P. D. R. Gamlin, 1998. Neurons in the posterior interposed nucleus of the cerebellum related to vergence and accommodation. *J. Neurophysiol.*, 79:1255–1269.
- Zhang, Y., L. E. Mays, and P. D. R. Gamlin, 1992. Characteristics of near response cells projecting to the oculomotor nucleus, *J. Neurophysiol.*, 67:944–960.
- Zhou, W., and W. M. King, 1998. Premotor commands encode monocular eye movements, *Nature*, 393:692–695.