

# Shared Target Selection for Combined Version-Vergence Eye Movements

VIVEK CHATURVEDI AND JAN A. M. VAN GISBERGEN

*Department of Medical Physics and Biophysics, University of Nijmegen, 6500 HB Nijmegen, The Netherlands*

**Chaturvedi, Vivek and Jan A. M. Van Gisbergen.** Shared target selection for combined version-vergence eye movements. *J. Neurophysiol.* 80: 849–862, 1998. Primates frequently make rapid binocular eye movements to reorient gaze in both direction and depth. To explain the unequal movements made by the two eyes, it often is assumed that they result from the combined action of a conjugate saccadic system and a vergence contribution. Clearly such a scheme can only yield coordinated binocular movements if both systems are guided by a shared or coupled target selection mechanism. To investigate the degree of cooperation at this level, we studied binocular refixations to target-nontarget double-stimuli in three-dimensional (3-D) space. Binocular eye movements were recorded in seven subjects using the scleral coil technique. In the experiments, 20% of trials were composed of a green target and a red nontarget, presented at the same time, but at different locations in 3-D space. These were alternated randomly with single-target trials (80%) in which the green stimulus was presented randomly at one of eight possible positions in 3-D space. Instructions to the subject emphasized either the speed or accuracy of response. Our findings show that typical features of the saccadic response to double-stimuli (bistability, averaging, and a speed-accuracy trade-off), as found in earlier two-dimensional studies, are also prevalent for initial binocular refixations to double stimuli in 3-D space. When the first saccadic response is directed to one of the two stimuli, the vergence system almost invariably makes the same choice. Likewise, when the saccadic system makes a short-latency averaging response, the vergence system shows a similar compromise. Statistical analysis shows a high correlation between saccadic and vergence target selection, strongly suggesting that the amplitude computation process of both subsystems is due to a common target selection stage that has access to information about stimulus location in 3-D space.

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## INTRODUCTION

This paper deals with the question of how the saccadic and vergence systems work together during coordinated binocular gaze-shifts in three-dimensional (3-D) visual space. There are often many potential targets in our immediate environment, and, accordingly, a choice must be made by each oculomotor subsystem to achieve proper binocular foveation. Logically, the question arises as to which neural mechanisms are involved in ensuring that the saccadic and the vergence system both select the same target. To investigate this problem, we presented subjects with a target/nontarget task whereby a number of combined saccade-vergence responses were elicited. By analyzing the extent to which correct and incorrect stimulus choices in the two subsystems were correlated, we could study the coupling of the target selection mechanisms. Earlier studies on saccade-vergence interactions, reviewed further on, have generally concen-

trated on the response dynamics, and this has led to various interpretations about how these systems coordinate the execution of binocular eye movements.

## *Saccade-vergence interactions*

Gaze-shifts in a natural environment generally require binocular refixations that have combined directional and depth components. In such responses, both the saccadic and the vergence subsystems are invoked to ensure that the respective lines of sight of the two eyes ultimately will intersect on the target of interest. It has become evident that, when tested in isolation, these two systems exhibit markedly contrasting dynamic characteristics (see for example: Collewijn et al. 1995; Erkelens et al. 1989; Yarbus 1967); saccades, responsible for the control of rapid changes of gaze in direction (version), are observed to be fast and conjugate (the eyes move equally in the same direction), whereas vergence responses (which rotate the eyes by equal amounts in opposite directions), required as a result of changing target distance, are disconjugate and relatively slow. These differences have led to the suggestion that conjugate and disconjugate eye movements use different neurophysiological substrates (Leigh and Zee 1983). The hypothesis of separate neural control systems has gained support with the discovery of vergence-related neurons in the midbrain (Mays et al. 1986).

These distinctions in response dynamics become less clear, however, in the more typical case where the gaze-shift requires a combined directional and depth change in the binocular point of fixation. Yarbus (1967) suggested that a binocular gaze shift could be described as a simple linear summation of two distinct processes. It has become apparent from later work that, during binocular refixations in 3-D space, there is actually a degree of interaction between the two subsystems and that the ensuing response is too complex to be resolved algebraically into a fast conjugate saccadic and a slow vergence component (Kenyon et al. 1980; Ono et al. 1978). In this situation, the disconjugate response is observed to be substantially faster than during a pure vergence response (Enright 1984, 1986; Erkelens et al. 1989; Maxwell and King 1992; Oohira 1993). Two hypotheses have been put forward, thus far, to explain this.

It has been proposed that the saccadic system could be responsible for this “facilitated” vergence phenomenon by producing unequal saccades in either eye. This suggestion entails that the saccadic system is actually capable of generating disconjugate movements (Erkelens et al. 1989). This hypothesis has received extra attention since a recent neuro-

physiological study (Zhou and King 1997) has shown that binocular eye movements may be under partial monocular and partial binocular control. It should be noted that the saccadic-depth contribution, proposed by this scheme, is incomplete in the majority of responses, so that an additional contribution of the slow vergence system is still needed. Furthermore, it cannot be excluded that this vergence contribution, clearly in evidence after the saccade, also may be present during the saccade. Another interpretation is that the vergence system is facilitated when a combined saccade-vergence response is elicited. Zee et al. (1992) recently proposed a model to account for this vergence facilitation. The model is composed of two parallel systems that are coupled through a shared initiation system. To explain the nonlinear interaction, it has been suggested that vergence burst-neuron activity is modulated by omnipause neurons during saccadic activity (Mays and Gamlin 1995, 1996; Zee et al. 1992).

Thus to explain how the fast depth component may arise, both hypotheses require a fast saccadic system and a slow vergence system. While the unequal saccade scheme involves a disconjugate saccadic system, the alternative scheme retains conjugate saccades but proposes an interaction with vergence. Although the saccadic and vergence contributions would be different, depending on which scheme is valid, it is clear that there are two systems that have to cooperate to bring the eyes to a specific target. Concentrating on this problem, the experiments in this paper have investigated the possibility of a common target selection stage driving both saccades and vergence.

#### Target-selection studies

Target selection has, until now, been studied in detail for the saccadic system. A number of frontal-plane double-stimuli studies (Becker and Jurgens 1979; Coren and Hoenig 1972; Findlay 1980, 1982; Ottes et al. 1984, 1985) have shown that the initial response of the saccadic system, depending on stimuli separation, can be to choose one of the two stimuli (bistability) or to direct the first saccade to a point between two targets (averaging). These experiments also showed that a speed-accuracy trade-off occurs whereby short-latency saccadic responses become increasingly error prone. Comparatively little work has been done regarding vergence target selection, but it is known that the vergence system can choose a target from several alternatives (Erkelens and Collewijn 1991).

By eliciting short-latency binocular responses in 3-D visual space, we have investigated to what extent target-selection for the saccadic and vergence systems is coupled. We describe experiments where both the saccadic and vergence system have to choose one target from two possible alternatives. A green target and a red nontarget stimulus were presented simultaneously in such a way that it should become evident whether the two systems could act independently or not.

## METHODS

### Eye movement recording

By placing subjects in the center of two perpendicular rapidly alternating magnetic fields, we could record binocular eye position

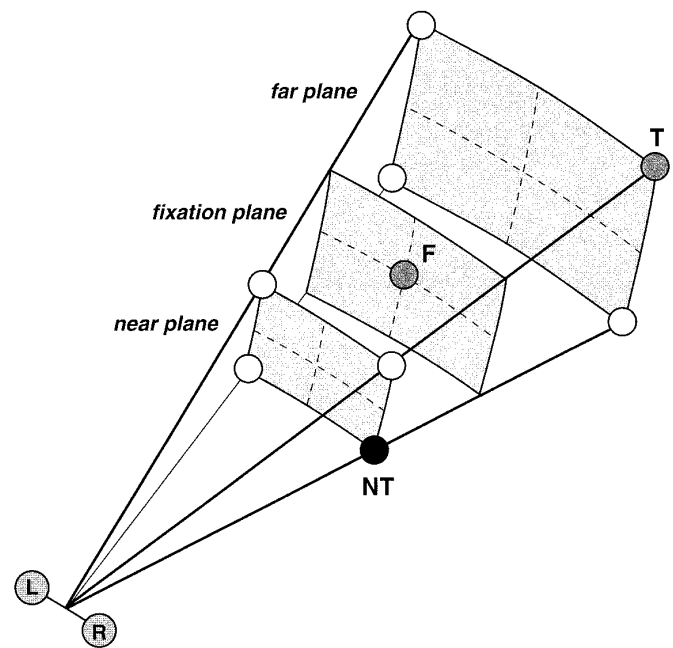


FIG. 1. View of light-emitting diode (LED) array used for 3-dimensional (3-D) target-selection task. Each trial began with the subject attending the green fixation point F, which was aligned with the cyclopean eye and had a target vergence of  $7.5^\circ$ . In all trials, the green target (T) could appear at any 1 of the 8 indicated corner locations: requiring a horizontal displacement of  $20^\circ$ , a vertical displacement of  $10^\circ$ , and a vergence change of  $2.5^\circ$ , with respect to the fixation point. In double-stimulus trials (20%), the red nontarget (NT) appeared, simultaneously with target T but at a location that was diametrically opposite in vertical direction and depth; the horizontal component was always kept the same. In the double-stimulus trial shown, T is right, up, and far away, whereas NT is right, down, and nearby. The eyes are denoted by L and R. Interocular distance (L-R) always was assumed to be 6.5 cm.

using the magnetic induction search coil technique (Collewijn et al. 1975; Robinson 1963). We used phase-sensitive detection techniques to demodulate the coil signals. The eye position data then were filtered, sampled, and stored on disk for further analysis (for details, see Chaturvedi and Van Gisbergen 1997).

### Calibration of binocular signals

During calibration the subject was instructed to fixate light-emitting diodes (LEDs) on a frontoparallel plane, placed at a distance of 125 cm from the subject. Thirteen horizontal and 13 vertical LEDs were positioned at different eccentricities (every  $5^\circ$ ), from the straight-ahead direction, spanning a range of  $\pm 30^\circ$ . The procedure was performed separately for each eye, and the center LED was aligned with the eye that was being calibrated. Both sets of recorded raw data were subjected to an off-line sinusoidal regression fit procedure to calibrate these signals. The horizontal angles of *version* (direction of the cyclopean eye) and *vergence* (angle between the lines of sight of the 2 eyes) were defined as being, respectively, the *mean* and *difference* of the two azimuth components. Interocular separation was assumed to be 6.5 cm.

### 3-D stimulus array and experimental design

After the coil calibration, a 3-D (horizontal, vertical, and depth) LED array (see Fig. 1) was mounted in front of the subject. The LEDs (5 mm diam) could be activated to be either green, to indicate the target, or red, to represent the nontarget. The position of the LEDs in the 3-D array was such that they required a horizontal

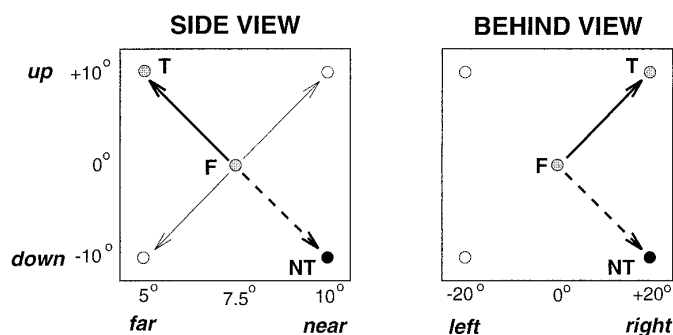


FIG. 2. Some theoretically possible saccade and vergence responses (seen from behind and from the side) for the double-stimulus configuration, depicted in Fig. 1. Extremes in potential behavior are shown to illustrate the concepts of concordant and discordant response modes. Concordant responses of both subsystems are shown in bold: the bold arrow from F to T denotes a correct response to the target location, whereas the dashed bold arrow is an incorrect response to the nontarget. Discordant responses (thin arrows) would occur if the saccadic and the vergence systems were to choose different stimuli (1 to T the other to NT). Because compromise responses are not shown, the set of examples is not exhaustive.

displacement of  $20^\circ$  (either leftward or rightward), a vertical displacement of  $10^\circ$  (either upward or downward) and a vergence change of  $2.5^\circ$  (to either a near or far surface), all with respect to the central fixation point (aligned with the cyclopean eye and having a target vergence angle of  $7.5^\circ$ ). All the LEDs in the array occupied positions on toroidal iso-vergent surfaces (Collewijn et al. 1988; Koenderink 1992).

Each stimulus sequence was 30 trials long and was composed of a number of single and double-stimuli trials. The latter (20% of trials) involved a green *target* (T) and a red *nontarget* (NT) presented at the same time but at different locations in 3-D space. The green target could be located at any of eight possible positions with the red nontarget having a diametrically opposite vertical and depth component value but with the same horizontal position. For example, when the target was presented in the right-far-upward position, the nontarget was located in the right-near-downward position (see Fig. 2). In this way, we could ascertain if discordant (where the saccade and vergence components made different target choices) or compromised responses (where the components went to neither the target or nontarget location but ended up somewhere in between the 2 stimulus positions) actually did occur.

Although the instruction in most experiments emphasized the need for a short-latency response to the green target, there were also a number of experimental sessions where the instruction emphasized the need for *accuracy* (rather than the speed) of binocular refixation. The results were used to analyze whether there was a speed-accuracy trade-off in 3-D. The double-stimuli trials were alternated randomly with single target trials in which a green LED was presented at various positions. The location of the initial green fixation point remained unchanged throughout the entire experiment and was always lit for a random period (ranging from 500 to 800 ms). Eye movement responses were recorded for a total duration of 2,000 ms in each trial, starting 50 ms before the offset of the central fixation LED. Experiments were carried out in dimly illuminated conditions such that the contours of the experimental room remained visible. Our use of real LED targets further ensured that a variety of depth cues were available (disparity, accommodation, relative size, and intensity).

### Data analysis

The velocity of the eye movements was calculated by differentiating the position signals. After filtering with a 33-point, 75-Hz Rabiner digital filter, a threshold level ( $30^\circ/s$ ) was applied to the

resulting velocity signal to detect saccades automatically; the results were always checked by visual inspection. For reasons that will be explained later, we concentrated the analysis on the binocular eye movement that occurred between the onset of the first and the onset of the second saccade (*1st movement* for short). Thus first movement onset was taken as the start of the primary saccade, and the end of the first movement was defined to coincide with the onset of the second (i.e., correction) saccade. If there was no correction saccade, or if the correction was delayed by  $>500$  ms, then the first movement offset point was taken at 200 ms (correction saccades for single and double-stimuli typically occurred 150–200 ms after the first saccade) after primary saccade offset. The *gain* of the initial eye movement was defined to be the ratio of actual eye displacement during the first movement to the total eye displacement required for a precise movement to the target. Accordingly, a correct movement had a gain of +1, whereas a response that was directed accurately to the nontarget had a gain of  $-1$ . By using this normalized gain measure, it was possible to pool responses to stimuli at all eight locations. In the analysis, we concentrated on the vertical component of the saccadic response (the horizontal component was typically an accurate leftward/rightward movement) and the vergence response. Trials with a wrong fixation at the start of a trial (with a discrepancy of  $\geq 5^\circ$  in the version angle or  $\geq 1^\circ$  in the vergence angle) and those having a predictive response (latency  $<75$  ms) were excluded from the analysis.

### Subjects

Experiments were carried out with seven male volunteers (AB, BW, JGO, HM, JVG, PH, and VC). Their ages ranged from 23 to 53 yr, and none had any known neurological or oculomotor disorders. Four subjects (JGO, HM, PH, and VC) wore corrective lenses during the experiment. Two subjects (JVG and VC) were familiar with the purpose of this study, whereas all the other subjects were kept naive. Before application of the coils, the surface of the eye was anesthetized with two drops of a local anesthetic (0.4% Novesine). Subjects were seated in a comfortable upright position while their heads were immobilized using a dental impression bitebar. All stimuli were viewed binocularly except during calibration. Experimental sessions generally lasted  $\leq 40$  min. Subjects were instructed to fixate the *green* target as *quickly* as possible (unless specified otherwise) but to refrain from making anticipatory responses.

## RESULTS

Our experiments were designed to investigate the target selection response for short-latency binocular refixations in 3-D visual space, with each response consisting of horizontal and vertical saccade components as well as a vergence component. To properly assess target selection for each subsystem during the double-stimulus task, it was essential to first analyze control responses to a single target.

### Control responses

In the control trials, each subject had to move the binocular point of fixation to one of eight possible single green targets, at the corners of a 3-D LED array (see METHODS). Each response trajectory started from the same fixation point in the center of this array. These eye movements always required a horizontal saccade (either rightward or leftward) with an up or down vertical component, which had to be combined with a divergence or a convergence movement

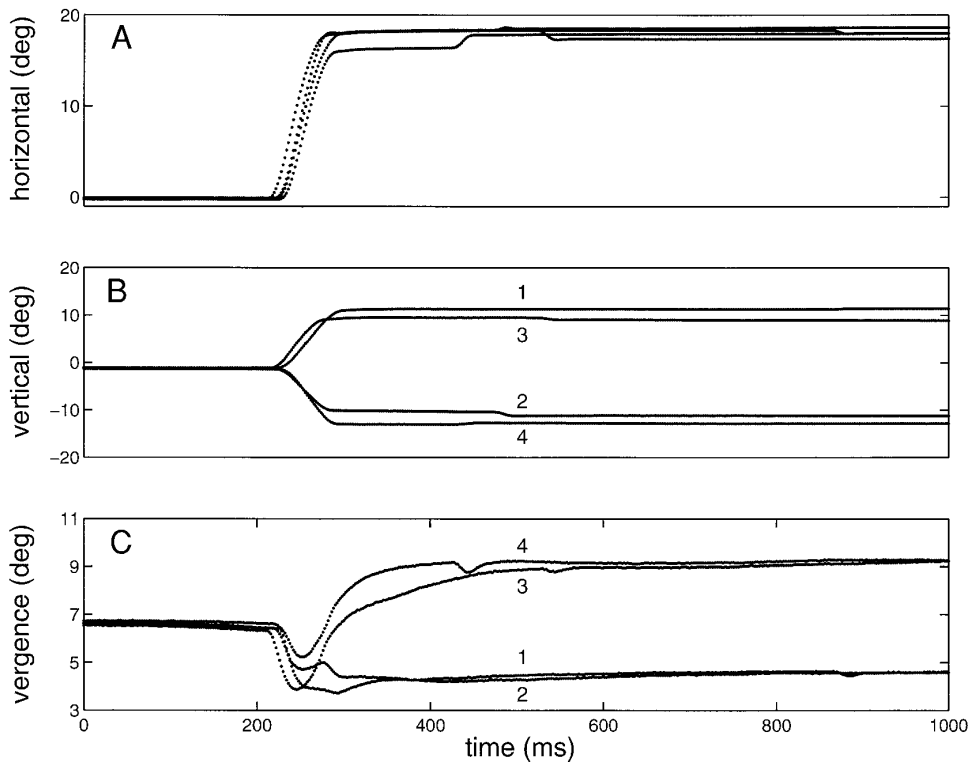


FIG. 3. Binocular eye movement responses of subject JVG to each of the 4 rightward targets in the 3-D LED array shown in Fig. 1. Shown are the horizontal version component (A), the vertical version component (B), and the vergence component (C). Response 1 was to the up-far target, response 2 was made to the down-far target, response 3 was directed to the up-near target, and response 4 was the eye movement to the target at the down-near corner. Rightward, upward, and convergence movements are depicted as positive deflections here and in all following figures. Note the occurrence of facilitated vergence during the saccade, and of a slow vergence phase after the saccade is completed. Transient divergence causes the eyes to initially move in the wrong direction for responses requiring convergence.

depending on whether the target appeared at the far or the near surface, respectively.

During the single-target controls, the saccades were observed to have simple temporal profiles with well-defined onsets and offsets (see Fig. 3, A and B). The accompanying vergence responses, on the other hand, were extended over a longer period of time and could be dissociated into two phases: an intrasaccadic movement and a slow postsaccadic component (Fig. 3C). It was not uncommon to see a presaccadic vergence component, but this contribution was typically very small and was not taken into consideration in our subsequent analysis. As can be seen in Fig. 3C, the intrasaccadic vergence movements to near targets contained a transient divergence episode that initially pushed the eyes in the wrong direction and that was later overtaken by an eye movement directed to the target. This transient divergence phenomenon is not completely understood but is thought to reflect a peculiarity of either eye muscle dynamics or the peripheral neural control system (Collewyn et al. 1988, 1997; Oohira 1993; Zee et al. 1992). For this reason, this phase of the response was not considered to be a true reflection of the target-selection system, and therefore we did not analyze it as such. Its presence, however, had clear consequences on how the eyes completed their depth movement. The corresponding trajectories in oculomotor space of the typical trials shown as distinct (vertical) saccade and vergence components in Fig. 3, B and C, respectively, are depicted in side view in Fig. 4. These figures plainly illustrate that, because of the effect of transient divergence, the first part of the vergence response may look similar for both converging and diverging responses. As a consequence of this phenomenon, convergence movements needed a more

sizeable postsaccadic vergence contribution than divergent responses. In the latter case, the eyes were already often close to target by the end of the first saccade.

The responses in our experiments, most notably those to double stimuli, often consisted of movement sequences where an initial movement could be followed by one or more later corrections. Because this sequence ultimately brings both eyes on target, the question arises at what point in time the target selection process should be judged. In the present analysis, we have made the assumption that the initial response to the stimulus (or stimulus pair) corresponds to the eye movements in the time interval between the onset of the first saccade and the start of the second saccade (i.e., the 1st movement; see METHODS). Experimental support for this assumption, indicating that the concept of first movement may be seen as the elementary unit of motor action, will be provided later.

Initial responses to all eight (4 on both the left- and the right-hand sides) control target positions, determined on the basis of this first movement criterion, are shown in Fig. 5. Each data point shows the endpoint of the binocular point of fixation at the end of the first movement. The scatterplots show clear clustering near each stimulus position. Thus the 1st movement endpoints from the control measurements could be distinguished clearly from each other even though their initial trajectories might have been quite similar.

As can be seen, the total vergence component in the first movement brought the eyes near to the target despite the fact that we found many diverse combinations of intra- and postsaccadic vergence contributions. These ranged from responses where the intrasaccadic part was almost negligible and the postsaccadic contribution was substantial to others

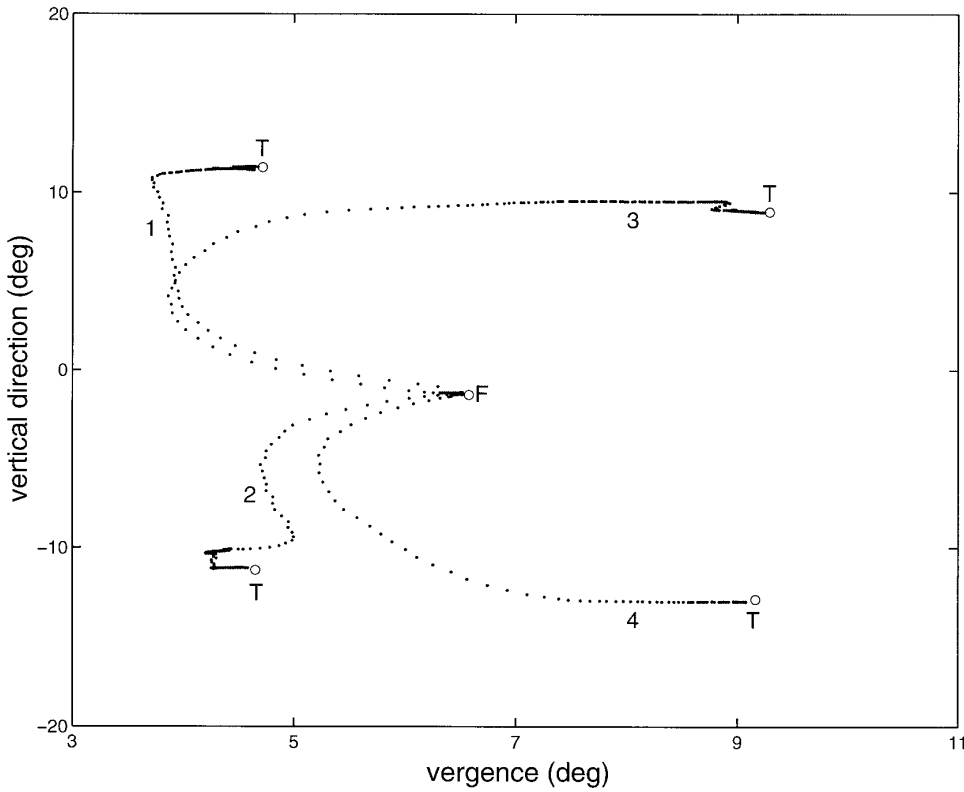


FIG. 4. Vertical version component and the vergence responses, from Fig. 3, have been plotted against each other to give an impression of the single-target control trajectories, in 3-D oculomotor space. Fixation point (F) was always the same. Responses 1 (up) and 2 (down) are directed to the far targets, whereas responses 3 (up) and 4 (down) are directed toward the near targets. Slight quantitative discrepancies observed in vergence angle fixations and vertical displacements are due to small calibration errors, differences in (subject) interocular separation, and slight head misalignments (with respect to the plane of regard). Sample interval was 2 ms.  $\circ$ , target positions recorded when the subject was required to fixate the LEDs during calibration.

where the intrasaccadic portion predominated. It is clear, therefore, that if we had taken primary saccade offset as the end criterion, one would not be able to obtain a correct impression of the vergence component of the binocular re-

fixation. Instead, the first movement concept, as we defined it, does not have this problem as the large postsaccadic vergence contribution makes up for the shortcomings of the intrasaccadic episode thereby separating the characteristics

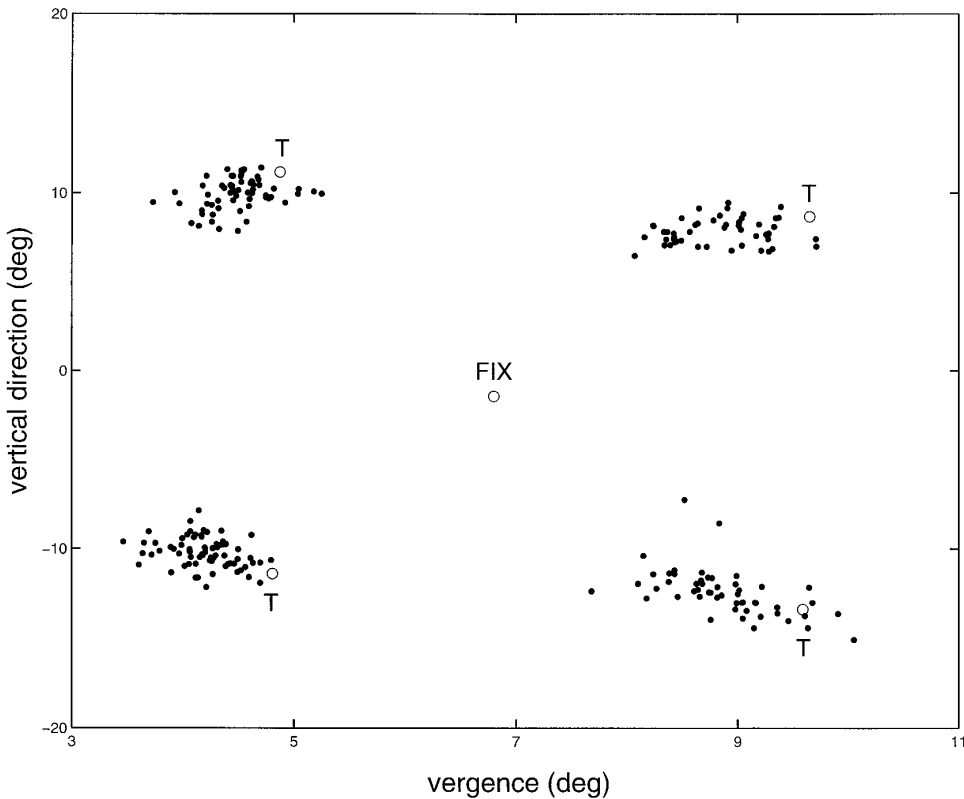


FIG. 5. Control response endpoints taken at the end of the 1st movement (i.e., onset of 2nd saccade). In this sideview plot (cf. Fig. 4), all controls on the right and the left side have been pooled. Subject JVG.

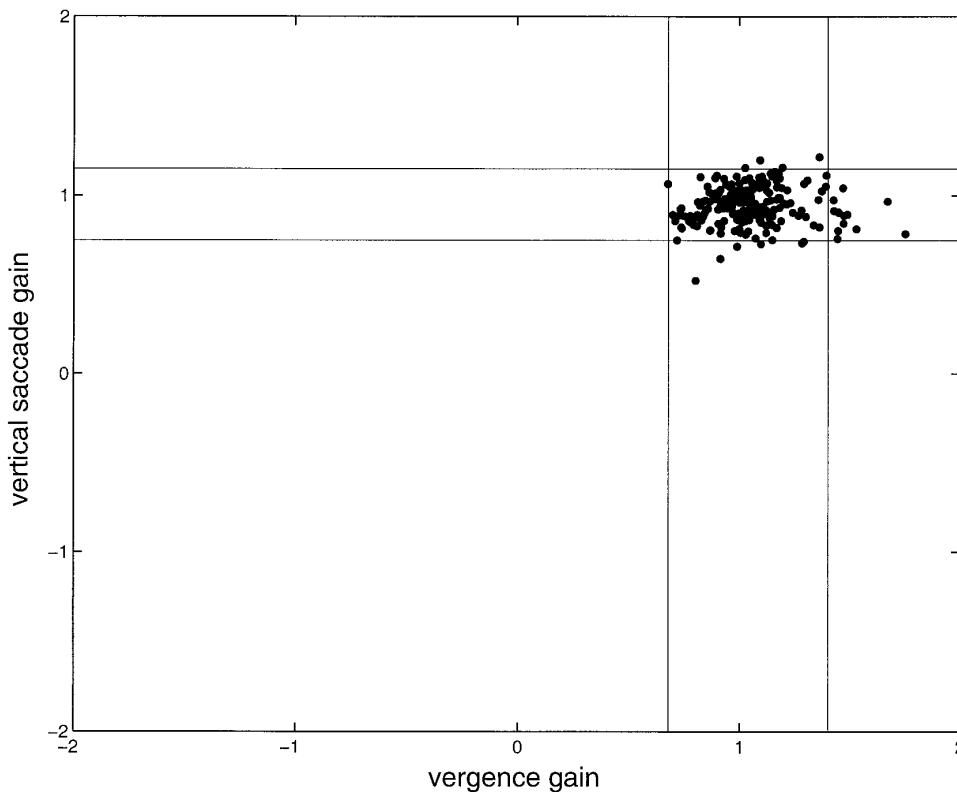


FIG. 6. Gain values (ratio of actual eye displacement to desired amplitude) of controls at the end of 1st movement. Correct and accurate responses should have a gain of unity. Note that both saccade and vergence responses have gains scattering around this value. Limits, taken to be twice the standard deviation values for both sets of gain components, give an indication of the variability of both the saccade and vergence responses for single-target control responses. These boundaries have been used to categorise double-stimulus responses as wholly correct or incorrect. An example of a vergence gain larger than +1 can be seen in *response 1* of Fig. 4. *Subject JVG*.

of near and far responses. In the ensuing analysis, our attention therefore will be focused on the first movement as reflecting the initial response of the refixation.

#### Normalization of the data

Because we wished to pool the results of the various types of trials (i.e., to targets that were positioned left/right, up/down, near/far), we standardized the data by computing gain values for both saccadic and vergence components of each first movement. Gain values were obtained by taking the ratio of the amplitude of the actual eye displacement to the required amplitude. These values, for saccades, were based on the vertical component because the required horizontal component, which was the same for target and nontarget, would not discriminate correct from incorrect responses. An accurately directed response of correct amplitude would have a gain of unity, whereas a wholly incorrect response, directed toward the nontarget, would have a negative gain of one. Note that the latter property of the gain measure holds as a consequence of the fact that target and nontarget always were presented on opposite corners of the 3-D LED array (i.e., corresponding to opposite version and vergence components). Not surprisingly, the pooled control responses of the saccadic and the vergence component, at the end of first movement, had gain values relatively close to unity (see Fig. 6). To characterize this variability in the control responses, we took the mean of all the values and computed  $\pm 2$  SD on each side. In evaluating the responses to double stimuli (see further), the resulting boundaries will be used to characterize responses as correct or incorrect. To provide an impression of the relative contribution of each portion of the total first movement, the intrasaccadic and end of first

movement gain values (and respective standard deviations) are shown in Table 1. As can be seen, the gain of the vergence response increases considerably during the postsaccadic episode. For the version response, the postsaccadic contribution, probably partly due to postsaccadic drift, is almost negligible.

#### Target/nontarget responses

To provide an impression of the wide range of possible responses to the target/nontarget double-stimulus task in 3-D space, we have selected three different trial responses to a stimulus configuration where the target was located downward and nearby, whereas the nontarget stimulus was upward and far away. The saccadic and vergence time profiles of each response are shown in Fig. 7, A–C. Again, the interpretation of the saccadic components is quite straightforward. *Response 1* is typical of a wholly incorrect initial response that is later followed by an opposite corrective saccade. In contrast, *response 3* is directly on target. *Response 2* is an example of saccade averaging. It should be noted that the horizontal component of these three responses was roughly comparable. As stated earlier, we have focused our efforts on the description of the vertical saccadic component because this is most indicative of the target-selection process. In comparison with the saccade response, the occurrence of transient divergence and the absence of clear-cut fixation periods tend to make the vergence response picture somewhat more complex to analyze. Nevertheless, it can be seen clearly, in Fig. 7C, that this subsystem has made stimulus choices that are very similar to those made by the saccadic system. For example, in *response 3*, the vergence system moves directly to the target too. In the trial where the

TABLE 1. Gain values of the vergence and version control responses

Subject	Number of Trials	Primary Saccadic Offset		End of First Movement	
		Vergence	Version	Vergence	Version
AB	192	0.61 ± 0.55	0.94 ± 0.18	0.95 ± 0.21	0.98 ± 0.10
BW	231	0.81 ± 0.33	0.99 ± 0.06	1.01 ± 0.20	1.00 ± 0.04
HM	96	0.59 ± 0.31	0.95 ± 0.09	0.92 ± 0.22	0.96 ± 0.08
JGO	199	0.91 ± 0.23	0.85 ± 0.11	1.01 ± 0.15	0.88 ± 0.11
JVG	219	0.80 ± 0.49	0.93 ± 0.11	1.04 ± 0.18	0.95 ± 0.10
PH	192	0.82 ± 0.52	0.96 ± 0.09	0.98 ± 0.14	0.97 ± 0.08
VC	177	0.61 ± 0.35	0.88 ± 0.14	0.92 ± 0.15	0.90 ± 0.12

Control responses of all subjects. Mean ± SD values of both saccade and vergence components of all trials are given for primary saccadic offset and for end of first movement. Comparison shows that the vergence gain at the end of the first movement is much closer to unity in all subjects, indicating the important contribution of vergence after first saccade offset.

saccade is wrongly directed (*response 1*), the vergence response also initially heads to the far nontarget before correcting itself. Interestingly enough, when the saccade makes an *averaging* response, then so does the vergence response (*response 2*). To study the suggestion emanating from these examples, that the target selections in the two subsystems are linked, we analyzed to what extent the gain values of saccadic and vergence responses were correlated.

A gain plot (for the same subject as shown in the controls of Fig. 6) of all first movements made in the target/nontarget task presents the data in a concise format (Fig. 8). The three responses presented in Fig. 7 are singled out here. *Response 3*, depicting unity version and vergence gains, indicates a completely correct initial refixation to the target, whereas *response 1* has negative gain values and appears to be directed toward the nontarget. Note that *response 2* has approximate gains of zero for both the saccade and vergence refixations, in line with the fact that it brought the eyes somewhere

in between target and nontarget. What becomes clear in this plot is that the saccade response in fact is coupled strongly to the vergence response. There is an evident cluster of points around the correct and incorrect gain points. Interestingly enough though, there is also a wide distribution of points between these extreme values that provides strong support for a coupling of the target-selection mechanisms of the two systems. The standard deviation limits shown here are those that were calculated previously from the control refixations (see Fig. 6). Note that most of the data points fall within these limits. It appears, therefore, that when the saccadic response makes a short-latency stimulus-directed response to either the target or the nontarget, the vergence system tends to make a similar choice. It can be observed that the saccadic system maintains its ability to produce averaging responses under circumstances where the short-latency refixations incorporate depth components. One of our most striking findings showing that target selection in both subsys-

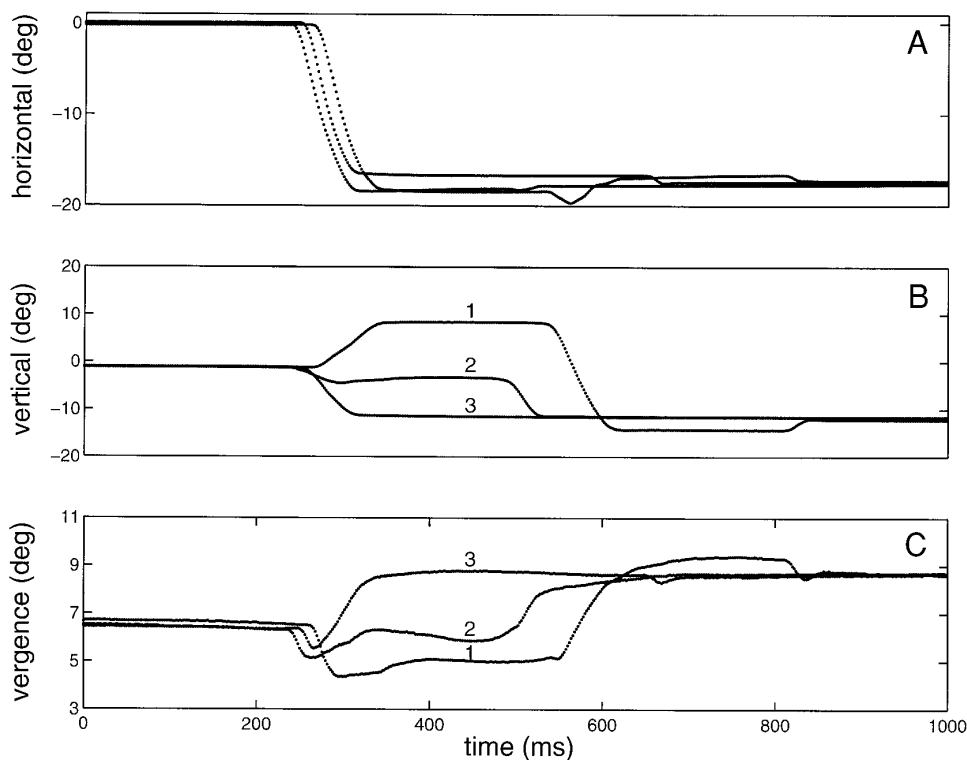


FIG. 7. Selected examples of responses from *subject JVG* to a double stimulus pair where the target was located nearby, downward, and to the left while the nontarget was presented faraway, upward, and also on the left. Same conventions have been used as in Fig. 3 (i.e., *A*: horizontal version; *B*: vertical version; *C*: vergence). Interpretation of the responses can be most easily made on the basis of the vertical saccade component. *Response 1* is initially wrongly directed and is followed by a large secondary saccade to the green target stimulus. *Response 3* is an example of a correct response. Finally, *response 2* shows averaging in the vertical saccade component and subsequently makes a corrective saccade. Vergence component shows a striking resemblance to the saccade counterpart. *Response 1* is similarly wrong and makes a diverging response to the far nontarget. This error is not corrected straightaway but is delayed until the later corrective saccade occurs. *Response 2* shows an averaging vergence response that coincides with the compromised saccade response.

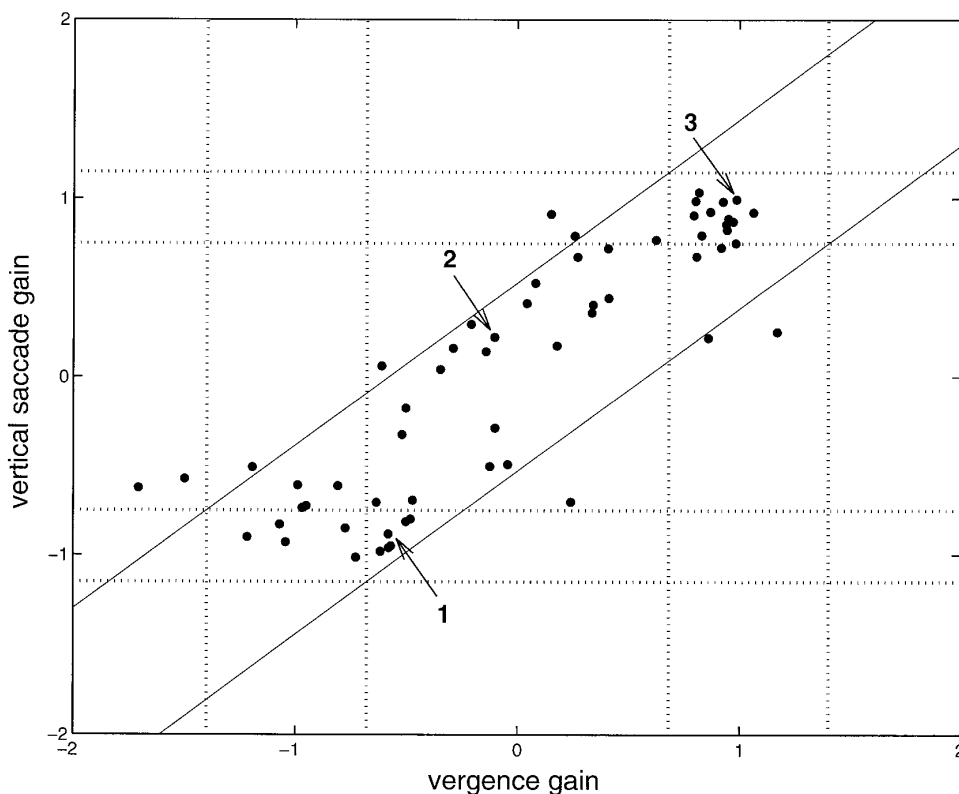


FIG. 8. Gain plot with all the data points from the target/nontarget paradigm showing a significant number of incorrectly directed and compromising responses for both saccades and vergence. Note that the saccade response is coupled closely to the vergence response. There are no discordant responses that exhibit near-unity gain values with opposite sign for saccade and vergence components. Limits (twice standard deviation), as defined in the controls of Fig. 6, have been drawn around both the correct (+1) and incorrect (-1) response values. Two oblique lines joining these limits denote the variability of the control refixations onto that of the double-stimulus responses. Most of the latter data points fall within these limits of variability, indicating that similar deviations from perfectly concordant behavior (equal gains in both subsystems) would occur in single target controls along the line from target to nontarget. Numbers in the plot refer to the three responses depicted previously in Fig. 7. Converging and diverging responses have a fairly even distribution of correct, incorrect and averaging responses. Horizontal component of these data points is always directed correctly and constant in size, with an approximate gain value around +1. *Subject JVG.*

tems is coupled is that when saccadic averaging occurs, the vergence refixation also shows a similarly compromised response. As far as we know, this is the first direct experimental demonstration that averaging also may occur in the vergence system. Because correct and incorrect target choices would be observed to have gain response values close to +1 and -1, respectively, this type of data presentation enables one to see, at once, whether the saccadic and vergence systems can show discordant behavior by directing their initial responses to different targets. This is, subsequently, seen not to be the case. Note that responses exhibiting opposite gain values (e.g., -1 and +1) for each subsystem were not observed. This hypothetical combination (where the systems would make diametrically opposing responses) would have meant that the binocular point of fixation would end up at a location where there was no stimulus at all (see Fig. 2).

Similar gain plots, depicting target/nontarget responses, are shown for other subjects. The subjects shown in Fig. 9, *A* and *B*, made predominantly correctly directed responses, and the endpoints are clustered around unity gain, although there are various incorrect and compromising responses in evidence. Figure 9*C* shows results from a subject who made only bistable (i.e., purely correct or incorrect) responses and where no averaging movements were elicited. The latencies were not significantly longer here than in other subjects. Figure 9*D* depicts a subject exhibiting a whole range of responses with again a strong suggestion of coupled target selection. Although most responses do fall within the boundaries of the diagonal band, there were also some violations of this principle. Figure 9*D*, *bottom right* (●), shows that there were some trials where the vergence refixation was

correct but the saccade was clearly misdirected. Although such examples of discordant behavior were atypical and rare (we saw a total of only 7 such examples among all the subjects that were studied), they are interesting as illustrations that independent target selection is in fact possible.

#### *Test for system independence*

In an effort to obtain an impression of the degree of association that each subsystem has with the other during the target/nontarget responses, we compared the two sets of gain values at the end of the first movement (as plotted in Figs. 8 and 9), using the statistical  $\chi^2$  test of independence. This test provides a measure of the discrepancy between the observed (i.e., recorded) values and the values expected on the basis of independence. By grouping the two variables under consideration, version and vergence gain, for each individual subject, we computed a  $\chi^2$  value that indicated how closely the two subsystem responses were related to each other during a double-stimulus task.

Our approach can be explained more clearly on the basis of the results, shown for one subject, in Fig. 8. Here we see that, for both axes, the gain values of +1 and -1 are bounded, on either side, by confidence limits (described earlier). Because the majority of the responses occur within these criteria, the occasional aberrant datapoint that lies beyond these limits is neglected. This enables us to define three distinct rows and three distinct columns of data points, in a contingency table for version and vergence gain, where the different types of responses are paired together. For example, in the top right cell, one can find 13 responses that are considered to have approximately unity gain (+1) for both

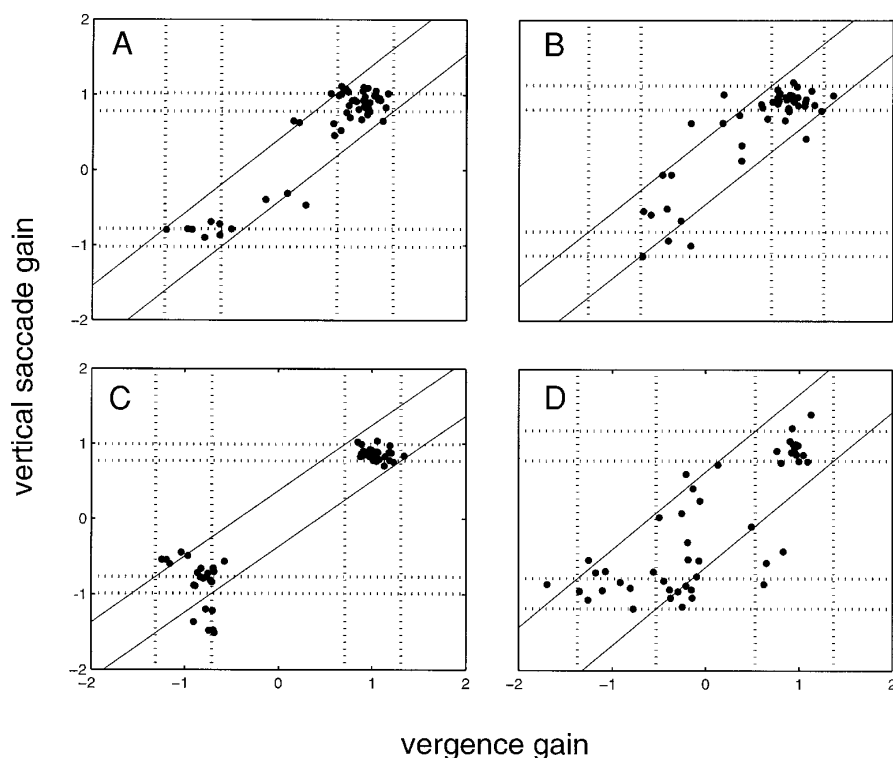


FIG. 9. Gain plots showing target/nontarget paradigm results in four other subjects. *A*: gain response plot of *subject VC* shows predominantly correct refixations along with a number of incorrect and compromised responses. *B*: *subject PH*, similarly, makes mostly target-directed responses. *C*: target selection behavior of *subject JGO* is bistable in nature. Responses are either entirely correct or entirely incorrect. There are no averaging responses at all. *D*: *subject AB* has a wide variability in responses. Note also a few exceptional discordant responses where the vergence gain is close to unity and the version gain is almost  $-1$ .

version and vergence; in the middle right cell, there are only four responses where the vergence is unity and the version has gain values between  $+1$  and  $-1$ ; in the bottom right cell, there are no responses where version has a negative gain with values around  $-1$  while vergence is still at unity gain. Using the marginal totals of these grouped values, we computed the cell frequencies that one should expect to obtain if the two variables are independent of each other. For example, the value calculated for the top right cell denotes the expected number of responses that will have both a version and vergence component close to unity gain. The difference between each observed and expected number is squared and divided by the expected value. These values are summed over all the cells to obtain the  $\chi^2$  value. The  $\chi^2$  value was significant ( $P < 0.01$ ) for all subjects, indicating that the null hypothesis, that no difference exists between the observed and expected values, could be rejected (see Table 2). Thus the version and vergence gain responses were not deemed to be independent of each other during a target selection task in 3-D space.

In line with this result, we found that the correlation coefficient taken for the gain values of the version and vergence responses (see Figs. 8 and 9), during the target/nontarget paradigm, was high ( $r > 0.75$ ) for all subjects (Table 2). This correlation provides additional support for an association between the two oculomotor subsystems during target selection. It should be noted, however, that some subjects had a high proportion of correct responses clustered around unity gain and this may have biased the results somewhat.

#### Corrective binocular eye movements after erroneous initial responses

As explained above, the analysis of binocular responses in this study leans heavily on what we have called the first

movement. The time limits that were used, first saccade onset to second saccade onset, require justification. The onset criterion was based on the strong impression, obtained from the recorded data, that the saccade and the vergence movement start virtually simultaneously. Cases where the movement in depth starts slightly earlier, with a slow drift, were sometimes noted, but the amplitude of these prelude vergence movements was always small (Chaturvedi et al. 1997). The offset criterion obviously had to be applied somewhere between first saccade offset and second saccade onset. We chose the latter temporal boundary to be sure that the postsaccadic vergence contribution was included.

The question arises whether this criterion is also adequate for the characterization of those double-stimulus responses where an initial incorrect response later was corrected. The typical pattern in such trials is that the second saccade is

TABLE 2. Statistical evaluation of the target/nontarget responses

Subjects	Number of Trials	$\chi^2$	Correlation Coefficient
<i>AB</i>	48	25.3	0.78
<i>BW</i>	58	21.3	0.86
<i>HM</i>	24	11.4	0.84
<i>JGO</i>	54	27.7	0.94
<i>JVG</i>	60	32.7	0.86
<i>PH</i>	48	22.2	0.86
<i>VC</i>	54	38.7	0.92

Target/nontarget responses of all subjects at the end of first movement. The  $\chi^2$  value and the correlation coefficients are given for all the trials. The term  $\chi^2$  indicates the degree of independence of either subsystem and is highly significant ( $P < 0.001$ ) for all subjects, except *subject HM*, who has a  $\chi^2$  value that is slightly less significant ( $P < 0.01$ ). The correlation coefficient of the data sets consistently has a high value.

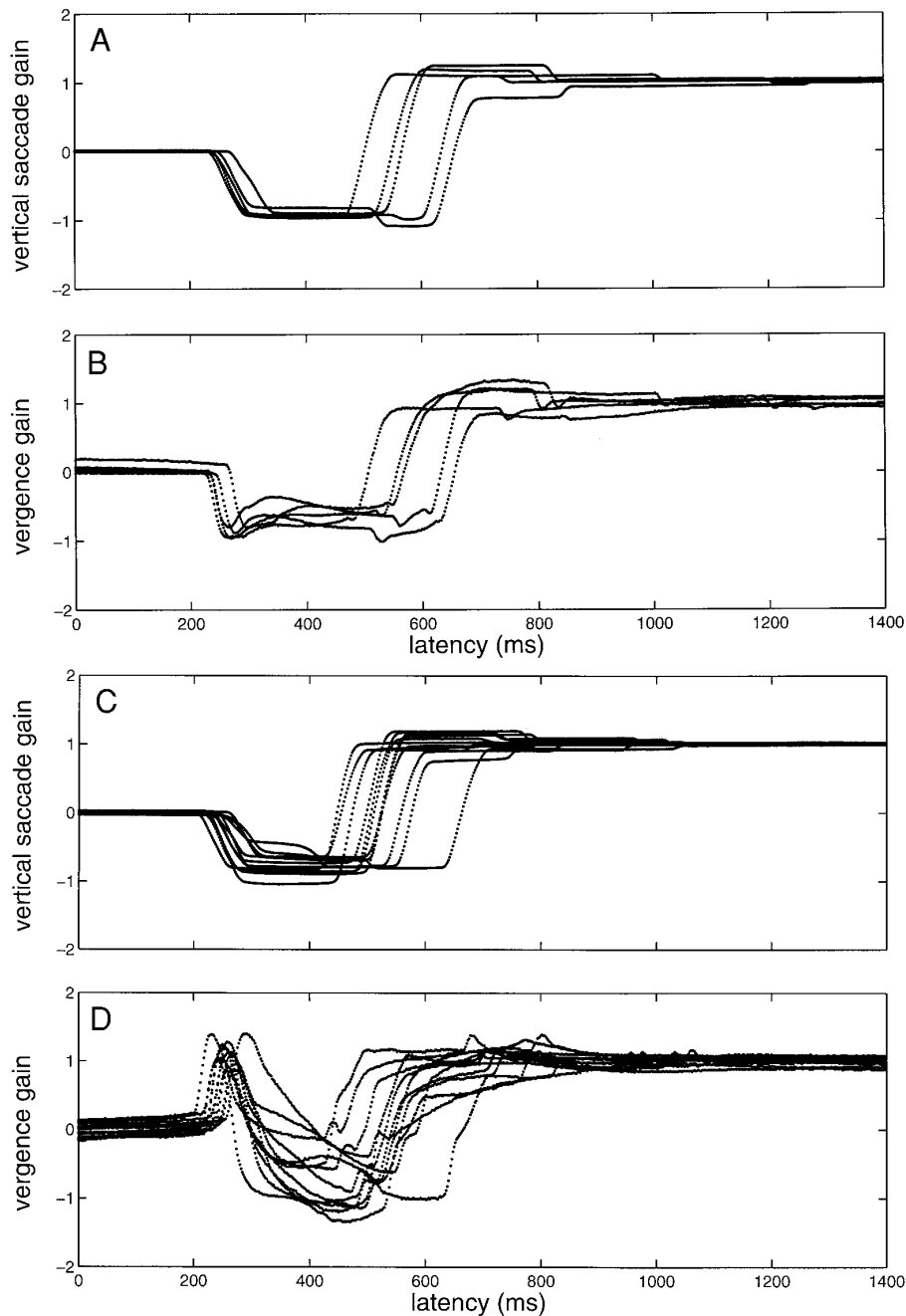


FIG. 10. Time course of corrective vergence movements to a near target (*A* and *B*) and a far target (*C* and *D*). *Subject JVG*. *A*: correction of initially wholly incorrect movements to a near target in the target/nontarget paradigm. Gain time course of the vertical version component showing erroneous 1st saccades to the far nontarget followed, after a fixation period, by a large correction saccade to the near target. *B*: gain time course of the vergence component. As in the saccade, the subject's initial response is to the nontarget. Note how the vergence correction is closely linked to the saccade correction, showing no consistent signs of movement from the nontarget in the fixation period before the corrective saccade. *C*: correction of initially incorrect movements (directed to a near nontarget 1st) to a far target in a target/nontarget paradigm. Gain time course traces for the vertical saccade responses. *D*: gain time course of the vergence component. In all traces, the transient divergence is very prominent initially but is then overtaken by vergence in the opposite direction to the near nontarget. Note especially that the incorrect vergence response persists throughout the entire 1st movement. Correction of the vergence response coincides with the 2nd saccade, directed toward the far target.

corrective but the question is what the vergence system does. Does it time its correction to coincide with the second saccade or can it reverse its ongoing trajectory earlier? If the latter was the case, the first movement as we defined it would be contaminated partly with what in effect would be an independently timed second movement of the vergence system. In fact, our data appears to provide little convincing support for this scenario. Rather, it actually seems as if the vergence system holds the incorrect position, or even continues its incorrect movement, until both systems initiate a simultaneous full-blown correction at the time of second saccade onset (see Fig. 10). We took the incorrect responses from Fig. 8 (selecting trials where both saccadic and vergence gains had values more negative than  $-0.5$ ) and

plotted their time courses as gain values. Accordingly, their final endpoints would be expected ultimately to attain a positive gain of  $+1$ , the starting points would have a gain of zero, and the initial incorrect responses would betray themselves by having negative gains. The incorrect responses to the far nontarget, in the case of near target presentation (Fig. 10, *A* and *B*), show how the corrective vergence response, after the initial wrong movement, is linked closely to the corrective saccade and does not start its corrective procedure prior to the saccadic component. Thus it is as if the system needs time to select a new target, which then is used to launch both systems into a new coordinated movement toward the new goal just as was previously observed in the first movement. This is seen more strikingly for incorrect

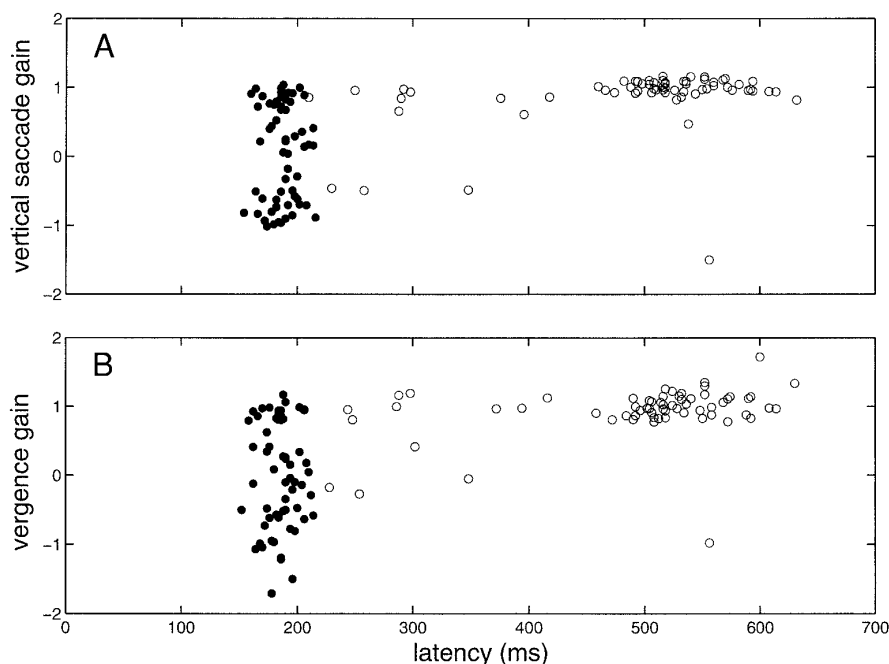


FIG. 11. Gain responses of 2 double-stimuli experiments, with different instructions, for *subject JVG*, are plotted here with respect to their latencies. *A*: saccadic onset was detected automatically by using a threshold value of  $30^\circ/\text{s}$ . This then was further checked by visual inspection. ●, taken from the experiment with the “fast” instruction, show that *short-latency* responses can have correct, averaging and incorrect endpoints of the first movement. ○, taken from an experiment with an “accurate” instruction, show that longer-latency responses are less error-prone and almost always have unity gain. *B*: vergence gain responses for the same trials.

responses to a near nontarget, when a far target was presented (Fig. 10, *C* and *D*). In this case, the responses have a markedly large initial transient divergence response, which thereby ensures that the entire wrong vergence movement is not fully completed by the time the corrective saccade is started. It is interesting to see that, in these cases, the correct vergence response clearly is initiated along with the corrective saccadic movement. Because similar results were seen for all subjects, we believe that the end of the first movement is a justifiable temporal measure when analyzing these combined saccade-vergence refixations.

#### *Speed-accuracy relationship*

For fast refixations, saccade and vergence target/nontarget latencies did not show an obvious relation to the gain value of the refixation observed at the end of the first movement. By including experiments where the instruction emphasized accurate rather than fast refixation, which provided responses with a much wider range of latencies, we found that refixations in 3-D visual space have a similar speed-accuracy trade-off as was previously found for the frontal plane. This was done for two subjects (*JVG* and *VC*). Figure 11 shows the saccade (*A*) and vergence (*B*) gain values for both short- and long-latency responses. Incorrect and compromised responses are generally only prevalent in a limited time frame for the “fast” refixations. When the instruction during the experiment urged an accurate refixation of the target without first going to the wrong stimulus, then the latencies became significantly longer, the responses became less error-prone, and the gain values of both saccade and vergence eye movements were predominantly around unity.

## DISCUSSION

### *Target selection in 3-D visual space*

This study was designed specifically to investigate how target selection mechanisms can ensure unified action when

the oculomotor system has to move in both direction and depth. It is widely believed that executing these refixations involves distinct oculomotor subsystems. There have been a number of studies that have concerned themselves with target selection in either the saccadic or the vergence system, but the problem of how the oculomotor system might handle the issue of target selection in combined saccade-vergence tasks has not been studied before.

Our double-stimulus task in 3-D required subjects to choose between a green target and a red nontarget, each of which was located at a differing location in direction and depth, such that errors in each subsystem could be assessed. Because little would be learned if subjects always made correct responses, they were pressed to make short-latency refixations. Our primary interest was to test the possibility of a common target selection stage controlling both the saccadic and the vergence systems to ensure that both eyes land on the same target. The results show that both the saccadic and vergence system behave in a spatially concordant fashion during these binocular refixations in 3-D visual space. This main conclusion applies equally well despite the fact that many of the responses showed averaging. The saccadic system already was known to show this remarkable behavior in short-latency responses to double stimuli in the frontal plane (Becker and Jurgens 1979; Coren and Hoenig 1972; Findlay 1980, 1982; Ottes et al. 1984, 1985). For large target separations, the saccadic system exhibits a bistable response, with saccades to either one stimulus or the other. When this separation is reduced, averaging saccades (directed to a location between the 2 stimuli) typically are found to be interspersed with responses near either stimulus. In other words, the initial saccadic response is not necessarily either correctly or wrongly directed but often lies in between the two stimuli.

Our results show that, for rapid binocular refixations to stimuli that have a distinct direction separation in 3-D visual space, the saccadic component of the visual response to the

double stimuli preserves the averaging characteristics seen previously by others in the frontal plane. We observed that the saccadic system, during a combined saccade-vergence refixation, can make either purely correct and incorrect initial responses but also can generate compromise responses in between the two stimuli. Interestingly, we also observed that the vergence component of the initial binocular refixation can, similarly, make different types of responses to stimuli that have a distinct depth separation. In other words the vergence response, just like the saccade, can be correctly or incorrectly directed or it can fall between the two stimuli as an averaging response. There was, however, a marked variability in responses among subjects to precisely the same stimuli. While some subjects showed this entire spectrum of responses, ranging from correctly directed to compromised to incorrectly directed refixations, other subjects exhibited purely bistable behavior (see Fig. 9).

Thus it appears that typical characteristics, which previously were seen only in the metrics of rapid saccadic responses to double stimuli in the frontal plane, also can be considered to be characteristics of rapid binocular refixations in 3-D visual space. An important further result, with obvious relevance for our main question, was that the seemingly stochastic behavior visible in each of the two subsystems was not independent. The highly significant correlation between saccadic and vergence target selection suggests a direct coupling between the two oculomotor systems (see Table 2).

Our analysis concentrated on the initial period of the binocular refixation, which we have called the first movement. Because of the way the stimulus presentation was designed, all responses required both a saccade and a vergence movement. Because the latter often outlasts the former, it is not a priori obvious whether the first movement concept, as we have used it, properly reflects the way the system actually works. By delimiting the first movement in this time window between the onset of the first and second saccade, we ensured that it included the slow vergence component that typically follows the first saccade. Using these time limits, we could define a statistical boundary that could be used to determine whether double-stimuli responses were fully correct or wholly incorrect. The analysis of initially incorrect responses (see Fig. 10) suggests that the eyes hold the resulting incorrect position for some time until a new target is defined which then elicits a combined corrective saccade-vergence movement. The fact that, in general, vergence did not start its corrective trajectory before the saccadic system did so indicates that the temporal limits for the first movement that we have defined are actually compatible with the apparently stepwise manner in which the oculomotor system executes the commands provided by the target selection stage.

#### *Relation to earlier target selection studies*

Although the target selection process of the saccadic system has been investigated extensively, relatively little is known about how the vergence system chooses its targets, and the question of how the two subsystems cooperate in target selection when presented with multiple stimuli has not been studied systematically at all.

It has been shown that subjects can easily change their binocular fixation from one visible object to another object

that is lying on a different depth surface (Erkelens et al. 1989). Erkelens and Collewijn (1991) have demonstrated that subjects can choose a small peripheral target, fixate it binocularly, and perceive it in binocular fusion, while disregarding other larger, more foveally located targets. Recently, Mallot et al. (1996) obtained indirect evidence (eye movements were not actually measured) that disparity-evoked vergence can be directed toward an average depth location. Their experiments, using stereograms with small disparity differences, were different from our experiments where the vergence response exhibited averaging-type behavior during large refixations to real targets.

Findlay and Harris (1993) had the novel idea to look at the averaging phenomenon from a binocular point of view. To this end, they studied binocular responses using a setup where refixations to a single target were elicited by changes in disparity. Their dichoptic study, which differs from our situation with real targets, specifically asked how the saccade was related to motor error in each eye. If fast eye movements had to bring the eyes directly on target (placed in the same hemifield of each eye), then unequal saccades in the two eyes would be necessary. Rather than seeing unequal saccades, Findlay and Harris observed that both eyes made the same saccade, aligning the cyclopean eye with the direction of the new target such that a correct refixation and, subsequently, binocular fusion of the target could be achieved through a follow-up pure vergence eye movement. This effectively means that the saccade coincided with the average of the two motor errors. This cyclopean saccade, therefore, did not contain any depth component and was purely conjugate. In our experiments, we have evoked comparable eye movements to real single targets at near and far locations. These responses, certainly those to distant targets, typically were composed of disconjugate saccades (see Fig. 3), which traversed a large part of the required depth during their trajectories, followed by final pure vergence movements. Similar findings on saccadic disconjugacy under these conditions have been reported extensively in the literature (Enright 1984, 1986; Erkelens et al. 1989; Maxwell and King 1992; Oohira 1993). It must be concluded that the disparity-driven "dichoptic" averaging effect, described by Findlay and Harris (1993), does not occur under our experimental conditions and pertains to a different issue than the averaging phenomenon observed in our study. The latter belongs to a different behavioral category that requires the use of multiple stimuli. Our main experiment, using the target/nontarget discrimination task, shows that binocular averaging in 3-D is just a generalization of saccadic averaging in the frontal plane. In both cases, the binocular point of fixation ends up at an intermediate position in 3-D space in between target and nontarget.

It was observed in the frontal plane speed-accuracy trade-off curves, documenting how saccade accuracy improved with latency (Ottes et al. 1985), that short-latency responses were unavoidably error prone. When the instruction to the subject was varied, by emphasizing either speed or accuracy of response, it was seen that errors could only be avoided if the saccadic response was delayed. Although it is reasonable to expect that this also will hold qualitatively for the present combined saccade-vergence refixations, it is conceivable, in theory, that the processing of depth and direction

information might have different temporal characteristics causing the saccadic and vergence speed-accuracy trade-offs to be different. To explore this, we extended our experiments to incorporate different instructions to test for this possible latency dependence. The results show that the notion of a speed-accuracy trade-off is equally valid for 3-D binocular refixations; this explains the occurrence of wrongly directed responses at short latencies. Quantitatively, the improvement in accuracy with latency seems quite comparable for the saccade and vergence components. It can be noted that the shortest latencies of the eye movements shown in our speed-accuracy trade-off plot (see Fig. 11) are longer than those in similar experiments done by Ottes and coworkers (1984, 1985). This may be related to the findings of Honda and Findlay (1992), who noted that during binocular viewing, saccades to targets in a different depth plane showed increased latencies.

#### *Neural mechanisms of target selection*

A fundamental problem in sensorimotor control concerns the neural mechanisms that are involved in the processes of visual target selection and the ensuing guided motor actions. A number of electrophysiological studies have used multiple stimulus paradigms in the frontal plane to investigate target identification and movement response selection before the generation of saccadic eye movements and to elucidate which neural areas are involved.

Recent work (Schall 1995; Schall and Hanes 1993; Schall et al. 1995) has demonstrated that the frontal eye fields (FEF), known to be responsible for the generation of goal-directed eye movements, may be highly involved in the process of saccade target selection. The FEF are known to have reciprocal connections to parietal areas in the so-called "dorsal" pathway, which is associated with identifying the spatial location (WHERE) of items in the visual scene. Other electrophysiological studies have investigated target selection in the superior colliculus (Basso and Wurtz 1997; Glimcher and Sparks 1992; Ottes et al. 1987). It appears that early neural activity occurs shortly after information regarding the metrics of the target becomes available and that this activity is modulated by target uncertainty. It cannot be excluded that the observed activity is a reflection of the response selection process already observed in FEF.

A recent study by Platt and Glimcher (1997) has provided evidence that saccade targets and visual distractors are represented by different levels of neural activity in the lateral intraparietal area (LIP) of the monkey. Area LIP would be an extremely interesting area to search for neural correlates of combined saccade and vergence target selection by virtue of the fact that this area was found to contain neurons with broad response fields that cover a 3-D volume of space with tuning curves at different preferred depths (Gnadt and Mays 1995). This type of neuron may code signals that are related to eye movements in direction (frontoparallel plane) and depth (distance from plane of fixation).

#### *Neural correlates of the averaging effect*

An interesting result of our study is that the vergence system was seen to make averaging responses when the

saccadic system does likewise. This new information puts the issue of how the averaging phenomenon arises in a different perspective, in as far as averaging previously was considered to be a purely saccadic phenomenon.

Electrophysiological studies in the monkey (Glimcher and Sparks 1993; Van Opstal and Van Gisbergen 1990) have shown that the superior colliculus is involved in a saccadic averaging response. On the basis of their findings, both studies proposed that the neural correlate for the averaging process can be found either at the level of the superior colliculus or at a location further upstream. The data presented in the aforementioned studies, along with the results obtained in our experiments, are compatible with the idea of a linked saccade-vergence target selection process that will now be discussed.

#### *Modeling aspects*

Models describing saccade-vergence interactions generally do not address the issue of target selection. They do suggest, however, that there may be coupling in the timing (WHEN system) of the two systems, through the activity of omnipause neurons (Mays and Gamlin 1995, 1996; Zee et al. 1992).

If one assumes that the direction and depth components of the binocular eye movement system are due to distinct oculomotor subsystems, the saccadic and vergence systems, the most parsimonious explanation of our findings would be that target selection and averaging occurs at an upstream stage where direction and depth are jointly represented. However, recent results presented by Zhou and King (1997), who found that oculomotor signals at the premotor level encode monocular saccadic eye velocity, indicate that the idea of a binocular version and vergence system probably is oversimplified. Although the study by Zhou and King (1997) provides a new view on saccade-vergence cooperation (see INTRODUCTION), refixations in 3-D still would require the cooperation of two systems: a fast system responsible for the change in direction and for part of the movement in depth and a slow postsaccadic vergence movement. As far as we know, there does not appear to be any studies that suggest that the slow postsaccadic and the fast intrasaccadic eye movement are generated by the same system. This, therefore, leads to a coordination problem, where both systems need to track the same target. Accordingly, one needs to explain how the slow vergence responses, which follow the initial saccade and appear to be continuations of the fast movement (see Fig. 10), arise. If the two systems always operate sequentially, the faster system theoretically could pass on its target selection information to the slower one, but it appears that a slow vergence movement actually may precede the saccade (Chaturvedi et al. 1997; Collewijn et al. 1997).

In summary, it seems reasonable to propose on the basis of our data that, to limit undesirable conflict, both subsystems (however specified in detail) are driven by a common target selection stage during binocular refixations in 3-D visual space.

#### *Conclusions*

This study has shown that the saccadic and vergence system work together closely in selecting targets and making

appropriate responses when stimuli are presented in 3-D visual space. This clearly is reflected in the instances when the saccadic system makes incorrectly directed or compromised responses. In each case, the vergence system makes a similarly directed response. This strong coupling in target selection by the two oculomotor subsystems is most parsimoniously explained by assuming a common selection system operating at a level where 3-D information is jointly available.

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Address for reprint requests: V. Chaturvedi, Dept. of Medical Physics and Biophysics, University of Nijmegen, P.O. Box 9101, 6500 HB Nijmegen, The Netherlands.

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