

Ocular Vergence Under Natural Conditions. I. Continuous Changes of Target Distance Along the Median Plane

C. J. Erkelens, J. Van Der Steen, R. M. Steinman and H. Collewijn

Proc. R. Soc. Lond. B 1989 **236**, 417-440

doi: 10.1098/rspb.1989.0030

References

Article cited in:

<http://rspb.royalsocietypublishing.org/content/236/1285/417#related-urls>

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Ocular vergence under natural conditions. I. Continuous changes of target distance along the median plane

BY C. J. ERKELENS¹, J. VAN DER STEEN¹, R. M. STEINMAN²
AND H. COLLEWIJN¹

¹*Department of Physiology I, Erasmus University Rotterdam, P.O. Box 1738,
3000 DR Rotterdam, The Netherlands*

²*Department of Psychology, University of Maryland, College Park,
Maryland 20742, U.S.A.*

(Communicated by G. Westheimer, F.R.S. – Received 21 November 1988)

Horizontal binocular eye movements of four subjects were recorded with the scleral sensor coil – revolving magnetic field technique while they fixated a natural target, whose distance was varied in a normally illuminated room. The distance of the target relative to the head of the subject was changed in three ways: (a) the target was moved manually by the experimenter; (b) the target was moved manually by the subject; (c) the target remained stationary while the subject moved his upper torso towards and away from the target. The rate of change of target distance was varied systematically in four levels, ranging from ‘slow’ to ‘very fast’, corresponding to changes in target vergence from about 10° s^{-1} to about 100° s^{-1} .

The dynamics of ocular vergence with regard to delay and speed were, under all three conditions, considerably better than could be expected from the literature on ocular vergence induced by disparity and/or blur.

When ‘very fast’ changes in the distance of the target were made, subjects achieved maximum vergence speeds of up to about 100° s^{-1} . Delays of these fast vergence responses were generally smaller than 125 ms. Negative delays, i.e. ocular vergence leading the change in target distance, were observed. The eyes led the target (i.e. predicted target motion) by about 90 ms on average, when the subject used his hand to move the target. Vergence tracking was almost perfect when changes in distance were produced by moving the upper torso. In this condition, the eye led the target by about 5 ms.

In the ‘slow’ and ‘medium’ conditions (stimulus speeds about $10\text{--}40^\circ \text{ s}^{-1}$) tracking was accurate to within $1\text{--}2^\circ$, irrespective of the way in which the target was moved.

In the ‘fast’ and ‘very fast’ conditions (stimulus speeds about $40\text{--}100^\circ \text{ s}^{-1}$), the accuracy of vergence tracking was better for self-induced than for experimenter-induced target displacements, and accuracy was best during voluntary movements of the upper torso. In the last case, ocular vergence speed was within about 10% of the rate of change of the vergence angle formed by the eyes and the stationary target.

The dynamics of convergent and divergent vergence responses varied considerably. These variations were idiosyncratic. They were consistent within, but not between, subjects.

Ocular vergence associated with attempted fixation of an imagined

target, changing distance in darkness, could only be made by two of the four subjects. The changes they could make were unreliable and poorly correlated with changes in the distance of the imagined target. Vergence changes did not occur when the distance to the target, imagined in darkness, was varied by keeping the target stationary and moving the torso back and forth.

In conclusion, when ocular vergence was studied under relatively natural conditions in which there were many cues to the distance of the target, oculomotor vergence was both much faster and much more accurate than could have been anticipated from previous studies done under more restricted stimulating conditions.

INTRODUCTION

Ocular vergence changes in response to three cues to motion in depth, namely the binocular depth cue called 'retinal disparity' (Westheimer & Mitchell 1956) and the monocular cues, 'blur' (Alpern & Ellen 1956) and 'change in size' (Erkelens & Regan 1986) of the retinal image. Each has been shown to be an *independent* driver of ocular vergence. Until now, studies concerned with the dynamics of ocular vergence have focused mainly on changes in a single, isolated motion-in-depth cue presented to a subject whose head was immobilized. All other cues to depth were eliminated by doing the experiments in darkened environments, effectively excluding all depth information except the particular cue under study. Normal viewing of motion in depth differs in three ways from viewing in such laboratory experiments: (1) commensurate changes occur in all motion-in-depth cues provided by the retinal images (changes in disparity do not occur without changes in blur or image size); (2) motion in depth may be caused partly or wholly by voluntary movements initiated by the subject, who can choose to grasp an object with his hand and move it nearer or farther away from his eyes, or choose simply to move his eyes nearer or farther from the object by moving his body relative to it; (3) a large repertoire of monocular and binocular cues to depth are clearly visible in normal viewing; these cues allow the distance of the target from the subject and the distance of the target from other objects and frames in the visual scene to be perceived veridically.

We studied ocular vergence responses made under relatively natural viewing conditions as a first attempt to determine whether vergence responses observed under such conditions could be predicted from descriptions of vergence responses to the isolated motion-in-depth cues that had been studied separately in previous experiments. We undertook to study vergence under relatively natural conditions because it has become increasingly clear in recent years that oculomotor performance, as well as its visual consequences cannot be predicted from studies undertaken under constraints that had been necessary and eventually became traditional in laboratory settings (Skavenski *et al.* 1979; Steinman & Collewijn 1980; Collewijn *et al.* 1983; Steinman *et al.* 1985).

The following conditions were employed: (1) a small target was moved back and forth in depth by the experimenter while the subject fixated it binocularly with his head immobilized; (2) the same target was moved back and forth in depth by

the subject while he maintained binocular fixation with his head immobilized; (3) the subject fixated the target, which remained stationary, while he moved his upper torso back and forth, thereby producing changes in the target's distance from his head. In the first two conditions, in which the experimenter's or the subject's hand moved the target, the target could be seen to change its distance relative both to the subject and to the other objects and frames in the visual scene. In the third condition, the target maintained its position in depth relative to other objects and frames in the visual scene, as the subject moved his upper torso so as to change the position in depth of his head relative to the target. Normal room illumination was maintained throughout this phase of the experimentation.

We found that ocular vergence in response to a target seen to be changing its position in depth in a normally lighted room, replete with natural cues to depth, had shorter delays and better dynamics than could have been expected from reports of previous experiments in which vergence responses were induced only by disparity and/or blur in an otherwise darkened environment. Changes in vergence often preceded changes in the distance of the target when the distance of the target was under control of the subject. The most accurate vergence tracking (smallest tracking error) was observed when voluntary movements of the upper torso, towards and away from a stationary target, provided the changes in the distance of the target. In this condition the target maintained its relative position in depth with respect to other objects and frames in the visual scene. We suspect that it was the stability of these cues to the relative position of visual objects, coupled with the relative simplicity of the requirements for coordinated motor control that pertained (eye-hand coordination was not required) that made it possible for the subject to track changes in the distance of the target almost perfectly in this condition.

METHODS

Subjects

Four subjects participated in the experiments. All had visual acuities of 20/20 or better, without (J.S. and R.D.) or with (A.M. and H.C.) refractive corrections, and none showed any ocular or oculomotor pathologies. Three of the subjects, an emmetropic male (J.S., age 34), a myopic male (A.M., age 26), and a myopic and presbyopic male (H.C., age 49), were very experienced in oculomotor research. The other subject, an emmetropic male (R.D., age 33), had served only occasionally in such experiments. The myopic subjects H.C. and A.M., who normally wear negative corrective spectacles, did not employ refractive correction during the experiments because they could see the targets well at the distances used. Avoidance of spectacle corrections, with their inherent changes in magnification, considerably simplified the geometrical-optical-oculomotor relations, which made it easier to study oculomotor performance.

Eye-movement-recording technique

The revolving magnetic field – sensor coil technique was used to record absolute horizontal eye positions of both eyes in space. The principle of this technique (Collewijn 1977) and the properties of the particular instrument used have been

described before (Collewijn *et al.* 1981). Briefly, sensor coils were attached to the eyes and a homogeneous magnetic field, rotating in the horizontal plane (field frequency 976 Hz), was generated around the subject. The phase of the alternating electric potentials induced by the field in a sensor coil mounted on the eye is linearly related to the rotating magnetic field's angular orientation. Absolute calibration is a particularly important feature of this technique. In the instrument used in these experiments, generation of the field and detection of the phase of the induced signals were controlled digitally. The noise level of the instrument was less than 40" and its linearity was better than 0.01% within its 360° range. Stability was better than 6" (for a fixed sensor coil) over periods from 1 s to 24 h. The maximum slewing speed of the digital output was 12000° s⁻¹. The instrument was not measurably sensitive to linear displacements of the coil within the range of translations studied in our experiments. Coils embedded in a self-adhering silicone annulus, as described by Collewijn *et al.* (1975), were used to measure the position of both eyes simultaneously. The stability of these coils on the eyes, when properly inserted, was documented by the inventors and reconfirmed in the present experimental apparatus (Collewijn *et al.* 1981).

Stimuli

The experiments were done in a normally illuminated room containing many rich cues to depth for distances up to about 2 m. The visual target consisted of a highly visible nail head (diameter 3 mm), which was painted white and attached to one end of a horizontal lever. The lever (figure 1) could rotate in the horizontal plane around a pivot, placed lateral to the target.

The length of the lever from the pivot to the target was 91.4 cm. The range of

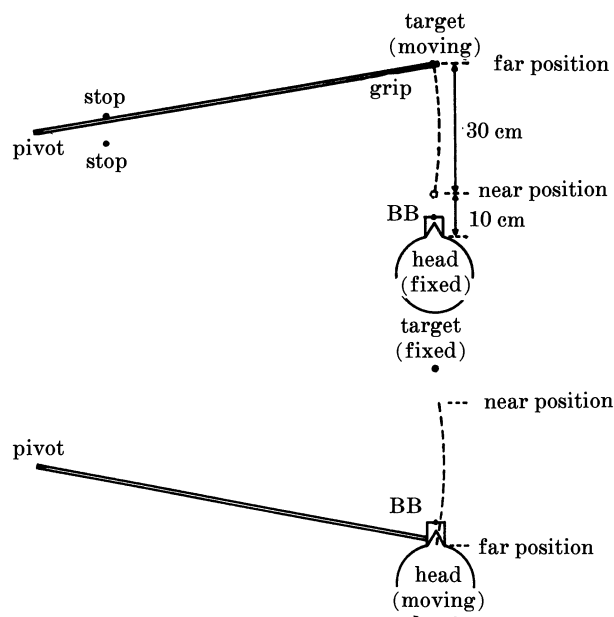


FIGURE 1. Top view of stimulus arrangement for manually induced target motion (top) and for head motion produced by moving the upper torso (bottom). In both situations, the subject's head was attached to a bite-board (BB).

rotation of the lever was limited by two stops, which marked target distances of 10 and 40 cm respectively. The subject was positioned in such a way that in the extreme positions the target was located in the median plane of the subject. Head position was stabilized by bite-boards with individually fitted dental impressions made of silicone rubber. Target distance was defined as the distance between the target and the midpoint of the line connecting the centres of rotation of the two eyes, which were assumed to lie 13.5 mm posterior to the front of the cornea. By using this definition of target distance, the angle of target vergence follows directly from the distance of the target because target vergence is defined as the angle subtended by the centres of rotation of the two eyes when converged on the target (Rashbass 1981). As the lever moved between the two stops, target vergence changed between about 9° and 36° . The exact angles were slightly different for each subject, depending on his interocular distance. The horizontal angular position of the lever was measured by a sensor coil attached to the lever directly above the pivot. Owing to the finite length of the lever, target movements were not restricted to the median plane, but followed a circular trajectory. The maximum deviation from the median plane was 1.6 cm (3.7° of visual angle) to the right when target distance was 25 cm.

Experimental procedures

Each experimental session began with a pair of calibration trials (one for each eye) during which absolute horizontal eye position was recorded while the subject fixated the centre of his pupil, which was reflected from a plane mirror oriented in the transverse plane. In this way, absolute monocular eye positions associated with a zero vergence angle could be estimated (i.e. the angle in which the visual axes of the eyes were parallel). Following this pair of monocular calibration trials, each session contained 20 binocular fixation trials in which the target distance was changed repeatedly in three different ways: (a) the target was moved manually, between the stops, by the experimenter; (b) the target was moved manually, between the stops, by the subject; (c) the target remained fixed at the far test position and the subject moved his upper torso towards and away from the target. In (c), the bite-board was attached to the horizontal lever to measure linear head position relative to the target. The bite-board could pivot around its attachment to the lever, and the stops limiting the extent of travel were removed to prevent damage to the teeth or apparatus. The trials in (b) and (c) (four in each condition) were repeated in complete darkness, while the subject attempted to fixate the imagined but now invisible target.

In each of these conditions four ranges of rate of change in target distance were used ('target speed'). They were described to the subject as 'slow', 'medium', 'fast' and 'very fast'. Generally, the maximum speed of target vergence ranged between 10 and 15° s^{-1} when the subjects adopted the instruction 'slow', between 20 and 30° s^{-1} for 'medium', between 40 and 60° s^{-1} for 'fast', and between 70 and 110° s^{-1} for 'very fast'. Each trial lasted 15 s. Trials were started when the subject indicated that he was ready. The horizontal angular positions of each eye, as well as the position of the lever, were each sampled at 122 Hz. The entire experiment was replicated during the same session for two subjects (R.D. and A.M.) and on different days for the other two subjects.

Data analyses

The stored samples represent the positions of the eyes relative to earth-fixed coordinates. Owing to the principle of the instrument, calibration of angular rotation was absolute and independent of the subject or the particular sensor coil used. Only standardization of the orientation of the annulus with respect to the visual axis was required. This zero position was estimated from the mean position of each eye during the initial calibration trials. The accuracy and precision of the instrument were very much better than the performance capacity of the oculomotor subsystem under study. Its noise level of 40" was determined by the limited number of discrete levels (16 bits) of the digital data that could be stored conveniently; instrument noise equalled the bit noise of the least significant bit. Velocities were simply calculated as the difference between adjacent samples, divided by the sampling interval. No filtering, smoothing or window techniques were used. Accordingly, the bit noise in the velocity signal was about 1.4° s^{-1} ($40'' / (\frac{1}{122} \text{ s})$). The effective bandwidth of both the position and velocity signals was 61 Hz.

In the off-line analysis target vergence was calculated from the data on the lever position and the interocular distance. Ocular vergence was calculated by subtracting the right horizontal eye position from the left horizontal eye position. The vergence error (i.e. absolute retinal disparity) was calculated by subtracting ocular vergence from target vergence.

RESULTS

General properties of ocular vergence

Continuous changes in target vergence almost always elicited smooth changes in ocular vergence; the rare saccades that were observed were small. The endpositions of ocular vergence under all conditions were commensurate with the endpositions of target vergence, i.e. our subjects were capable of covering the entire convergence range of about $9\text{--}36^\circ$ required by changes in the distance of the target. Thus our range of target vergence did not exceed the static mechanical or neural limits of ocular vergence. In the present experiments, we were particularly concerned with the *dynamic* capacity of the vergence subsystem when it is examined under demanding circumstances, i.e. the conditions present during 'fast' and 'very fast' target motions. These conditions will therefore receive special emphasis in the description of the results.

In general, vergence error increased progressively as the speed of change in target vergence increased. Responses to repeated changes in target vergence were very reproducible with regard to maximum speed as well as with regard to delay. Vergence responses did not improve within sessions or throughout the experiments. This lack of any progressive improvement, either in speed or delay, implies that the vergence system did not 'learn' from its previous movements. Our observations therefore probably approximate the capacity limit of the normal vergence subsystem.

The dynamics of convergent and divergent movements could show considerable

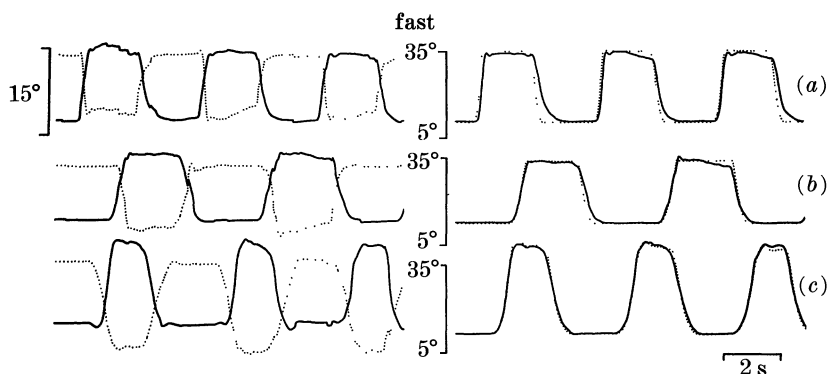


FIGURE 2. Eye movements of subject R.D. made in response to 'fast' changes in target distance. The left panels show movements of the left (continuous lines) and right (dotted lines) eye. The right panels show the corresponding changes of ocular vergence (continuous lines) and target vergence (dotted lines). Upward deflections: rightward monocular movement (left panels); convergence (right panels). (a) Target moved by the experimenter; (b) target moved by the subject; (c) changes in target distance by movements of the upper torso.

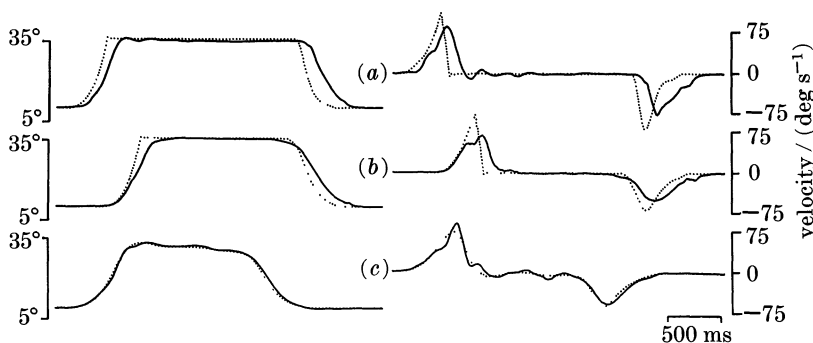


FIGURE 3. Position (left panels) and velocity (right panels) profiles of ocular vergence (continuous lines) of subject H.C. made in response to 'very fast' changes in target vergence (dotted lines). (a) Target moved by the experimenter; (b) target moved by the subject; (c) changes in target distance induced by movements of the upper torso.

differences, which were consistent within, but not between, subjects. Convergent movements were faster in two of the four subjects, whereas the opposite was the case in the other two subjects. One direction of vergence is clearly not necessarily superior to the other under our conditions and the idiosyncracies observed suggest that there is no inherent superiority of one or the other response. Representative responses to 'fast' (about 45° s^{-1}) changes in target vergence are shown in figure 2; examples of performance in the 'very fast' condition (changes in target vergence faster than 75° s^{-1}) are shown in figure 3. The velocity profiles in figure 3 show that ocular vergence movements oscillated with a period of about 200 ms under all three experimental conditions. Such oscillations are typical of vergence responses induced by disparity (Westheimer & Mitchell 1956).

Speed of vergence tracking

The speed of ocular vergence of each of the four subjects was considerably higher than has ever been reported in the literature. Maximum speeds of more than $100^{\circ} \text{ s}^{-1}$ occurred in occasional trials, a value three to five times higher than the maximum described previously for disparity-induced vergence (Erkelens 1987).

The *maximum* speed of target and ocular vergence was determined for each response; the means and s.d. of these maxima (and their ratio) are summarized in table 1, separately for the different subjects and conditions. Convergence and divergence were pooled because the differences among these were not systematic. The highest mean maximum ocular vergence speed ($73^{\circ} \text{ s}^{-1} \pm 14^{\circ} \text{ s}^{-1}$) was attained when the experimenter moved the target 'very fast'. Target vergence speed was also highest ($117^{\circ} \text{ s}^{-1} \pm 15^{\circ} \text{ s}^{-1}$) in this condition.

Maximum mean ocular-vergence speed amounted to a considerable fraction of maximum mean target-vergence speed; this fraction was of the order of 0.9 for 'slow' changes in distance and it tended to decrease as target-vergence speed increased, reaching values around 0.7 when target-vergence speed was 'very fast'.

These maxima lasted only briefly in the stimulus as well as in the response. We also calculated the *average* speeds of ocular and target vergence over the whole interval in which it was changing so as to provide a more complete description of the vergence subsystem's overall capacity. The onset and offset of movements in the target vergence and ocular vergence traces were detected by a velocity criterion of 5° s^{-1} in combination with a minimum movement duration of 30 ms. This velocity threshold was well above the noise level of $2.8^{\circ} \text{ s}^{-1}$ of the vergence traces (see Methods).

Average ocular vergence speeds are plotted as a function of average target vergence speed in figure 4, separately for the four subjects and three conditions. Accurate tracking (disregarding delays) would require the data points to lie on the diagonal lines, reflecting a 1:1 relation between the eye and the target. This situation was closely approximated by all four subjects in all three conditions with target vergence speeds up to about $25^{\circ} \text{ s}^{-1}$. For higher target speeds, the average ocular vergence speeds of subjects J.S. and A.M. saturated at about $30^{\circ} \text{ s}^{-1}$ despite the fact that these subjects could reach maximum ocular vergence speeds of more than $60^{\circ} \text{ s}^{-1}$ (see table 1). For the other two subjects, H.C. and R.D., mean ocular vergence speeds did not saturate until target speed was above $50^{\circ} \text{ s}^{-1}$.

Accuracy of vergence tracking

The mean positional vergence tracking error was calculated to summarize the accuracy of ocular vergence. The time interval, over which the vergence error was averaged, started at the onset of target movement and ended at the offset of the ocular vergence response, which was determined by using the velocity-duration criterion described above. The boundaries of the time interval for averaging vergence error could only be roughly estimated for 'slow' changes in target vergence (our accuracy was not better than ± 100 ms). However, at 'slow' target speeds the duration of target movement was so long (about 4 s) that this inaccuracy in the determination of the time interval hardly affected the mean value

TABLE 1. MEAN MAXIMUM SPEEDS IN DEGREES PER SECOND (\pm S.D.) OF OCULAR VERGENCE (V_o), TARGET VERGENCE (V_t) AND THEIR RATIO (V_o/V_t) FOR FOUR SUBJECTS, FOUR SPEED RANGES AND THREE MOTION CONDITIONS

| speed range | subject | experimenter, manual | | | subject, manual | | | subject, torso motion | | |
|-------------|--------------------------|----------------------|--------------|-----------------|-----------------|--------------|-----------------|-----------------------|-------------|-----------------|
| | | V_o | V_t | V_o/V_t | V_o | V_t | V_o/V_t | V_o | V_t | V_o/V_t |
| 'slow' | A.M. | 7 \pm 1 | 9 \pm 1 | 0.78 | 14 \pm 3 | 16 \pm 4 | 0.88 | 11 \pm 3 | 11 \pm 5 | 1.00 |
| | H.C. | 14 \pm 5 | 12 \pm 3 | 1.17 | 14 \pm 3 | 15 \pm 3 | 0.93 | 13 \pm 2 | 13 \pm 2 | 1.00 |
| | J.S. | 15 \pm 7 | 14 \pm 6 | 1.07 | 12 \pm 3 | 15 \pm 6 | 0.88 | 11 \pm 2 | 11 \pm 2 | 1.00 |
| | R.D. | 10 \pm 2 | 12 \pm 1 | 0.83 | 12 \pm 2 | 16 \pm 4 | 0.75 | 11 \pm 2 | 12 \pm 3 | 0.92 |
| | overall means \pm s.d. | 12 \pm 4 | 12 \pm 3 | 0.96 \pm 0.19 | 13 \pm 2 | 16 \pm 1 | 0.86 \pm 0.08 | 12 \pm 1 | 12 \pm 1 | 0.96 \pm 0.04 |
| 'medium' | A.M. | 18 \pm 2 | 22 \pm 2 | 0.82 | 26 \pm 14 | 37 \pm 21 | 0.70 | 25 \pm 4 | 25 \pm 4 | 1.00 |
| | H.C. | 19 \pm 2 | 20 \pm 2 | 0.95 | 21 \pm 3 | 24 \pm 4 | 0.88 | 23 \pm 3 | 27 \pm 3 | 0.85 |
| | J.S. | 19 \pm 6 | 22 \pm 3 | 0.86 | 12 \pm 2 | 16 \pm 3 | 0.75 | 14 \pm 4 | 14 \pm 3 | 1.00 |
| | R.D. | 19 \pm 2 | 22 \pm 3 | 0.86 | 20 \pm 8 | 26 \pm 8 | 0.77 | 16 \pm 5 | 18 \pm 6 | 0.89 |
| | overall means \pm s.d. | 19 \pm 1 | 22 \pm 1 | 0.87 \pm 0.06 | 20 \pm 6 | 26 \pm 9 | 0.78 \pm 0.08 | 20 \pm 6 | 21 \pm 6 | 0.94 \pm 0.08 |
| 'fast' | A.M. | 39 \pm 6 | 52 \pm 14 | 0.75 | 50 \pm 12 | 66 \pm 17 | 0.76 | 54 \pm 8 | 56 \pm 9 | 0.96 |
| | H.C. | 32 \pm 12 | 40 \pm 16 | 0.80 | 44 \pm 6 | 46 \pm 10 | 0.96 | 38 \pm 5 | 43 \pm 7 | 0.88 |
| | J.S. | 37 \pm 4 | 53 \pm 15 | 0.70 | 27 \pm 5 | 35 \pm 9 | 0.77 | 28 \pm 3 | 32 \pm 4 | 0.88 |
| | R.D. | 36 \pm 4 | 49 \pm 7 | 0.69 | 37 \pm 8 | 38 \pm 6 | 0.97 | 41 \pm 6 | 44 \pm 10 | 0.93 |
| | overall means \pm s.d. | 36 \pm 4 | 49 \pm 6 | 0.74 \pm 0.05 | 40 \pm 10 | 46 \pm 14 | 0.87 \pm 0.12 | 40 \pm 11 | 44 \pm 10 | 0.91 \pm 0.04 |
| 'very fast' | A.M. | 62 \pm 17 | 100 \pm 14 | 0.62 | 56 \pm 9 | 96 \pm 24 | 0.58 | 63 \pm 6 | 75 \pm 9 | 0.84 |
| | H.C. | 86 \pm 14 | 135 \pm 32 | 0.64 | 71 \pm 7 | 108 \pm 16 | 0.66 | 71 \pm 15 | 79 \pm 23 | 0.90 |
| | J.S. | 60 \pm 18 | 112 \pm 21 | 0.54 | 55 \pm 12 | 84 \pm 19 | 0.65 | 54 \pm 9 | 90 \pm 15 | 0.60 |
| | R.D. | 84 \pm 26 | 119 \pm 15 | 0.71 | 53 \pm 12 | 69 \pm 15 | 0.77 | 62 \pm 9 | 72 \pm 9 | 0.86 |
| | overall means \pm s.d. | 73 \pm 14 | 117 \pm 15 | 0.63 \pm 0.07 | 59 \pm 8 | 89 \pm 17 | 0.67 \pm 0.08 | 62 \pm 6 | 79 \pm 8 | 0.80 \pm 0.13 |

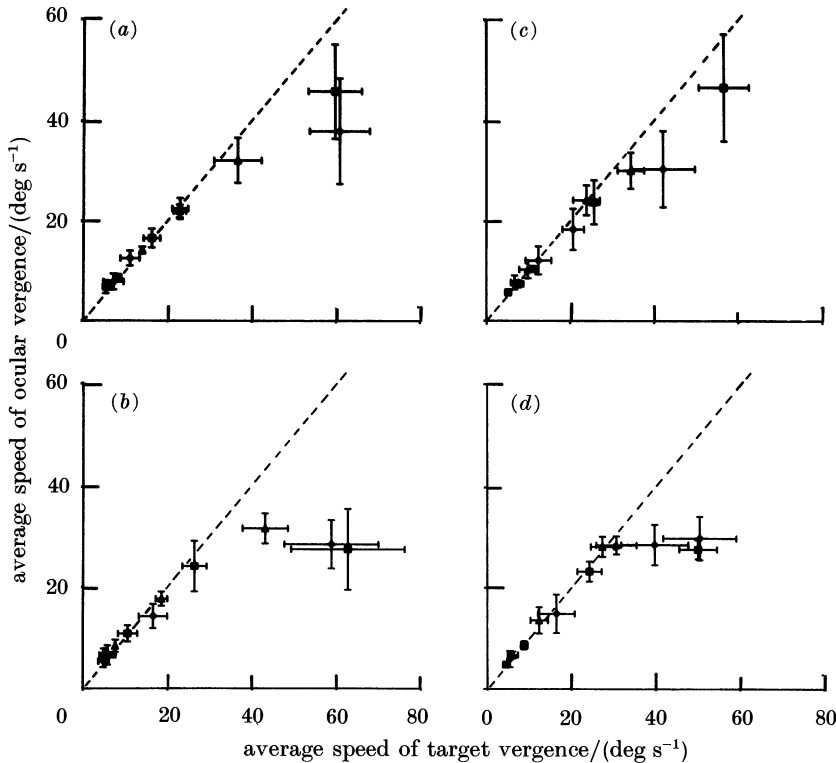


FIGURE 4. Average speed of each of the four subjects' ocular vergence (± 1 s.d.) as a function of the average speed of target vergence (± 1 s.d.) in each of the four speed ranges used. (a) H.C.; (b) J.S.; (c) R.D.; (d) A.M. Squares: target moved by experimenter; diamonds: target moved by subject; triangles: changes in target distance induced by movements of the subject's upper torso.

of the vergence error. The mean vergence errors, averaged over convergent and divergent movements as a function of the mean speed of target vergence, are shown in figure 5.

The most important message conveyed by figure 5 is that the average absolute disparity of the target (vergence error) did not exceed 1° for average target vergence speeds up to 20° s^{-1} and remained below 2° for target vergence speeds up to 40° s^{-1} . Inter-subject differences were negligible throughout this range. For the fastest changes in target vergence (mean speed $40\text{--}60^\circ \text{ s}^{-1}$), mean vergence error rose sharply to $4\text{--}6^\circ$. This is particularly clear in the data of subjects J.S. and A.M., whose ocular vergence speeds tended to be lower than those of subjects H.C. and R.D. (see figure 4). J.S. and A.M.'s lower ocular vergence speeds could be expected to produce larger vergence positional tracking errors when the target moved faster than 40° s^{-1} .

Differences among the different ways of changing target distance

Ocular vergence showed remarkable differences under the three experimental conditions. Some of these differences are sufficiently large to be visible even in the

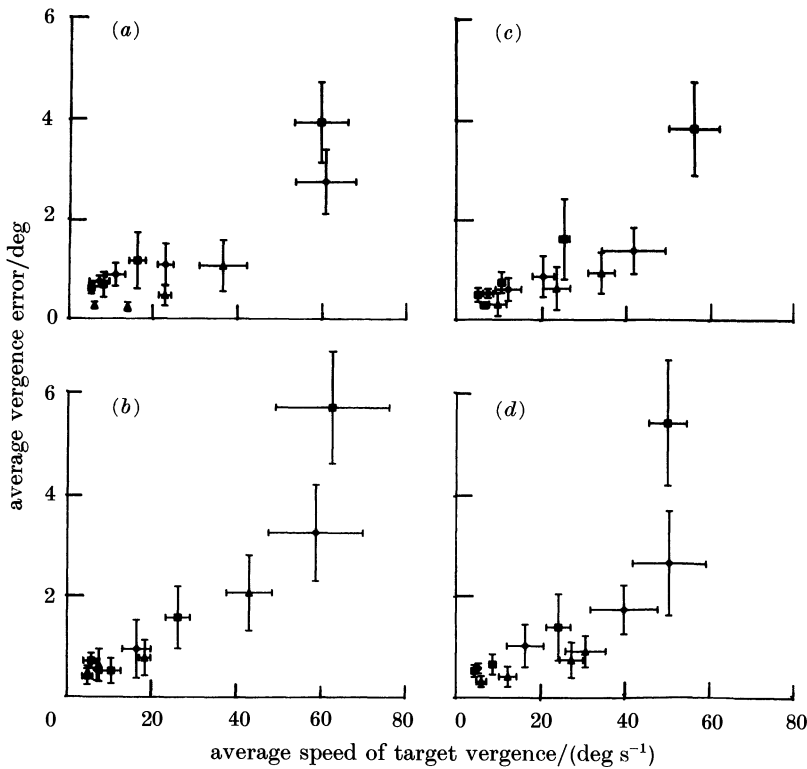


FIGURE 5. Mean vergence errors of each of the four subjects (± 1 s.d.) as a function of the average speed of target vergence (± 1 s.d.) in each of the four speed ranges used. (a) H.C.; (b) J.S.; (c) R.D.; (d) A.M. Squares: target moved by the experimenter; diamonds: target moved by the subject; triangles: changes in target distance induced by movements of the subject's upper torso.

raw recordings of vergence position and velocity as a function of time reproduced in figures 2 and 3. Generally, tracking was more accurate for subject-generated than for experimenter-generated target motion. For subject-generated target motion, vergence tracking was better during motion of the upper torso than during manual displacement of the target. These differences in accuracy were caused by systematic differences in the speed, as well as in the timing of the ocular vergence responses.

Differences in speeds

A comparison of the maximum vergence speed under the three conditions can be made by scanning horizontally through table 1. The most straightforward comparison can be made for the 'slow', 'medium' and 'fast' stimulus speeds because, in these cases, rather similar target vergence speeds were obtained under all three conditions. In the 'very fast' range, target speeds generated manually by the experimenter proved to be systematically higher than those generated by the subject. The ratios of maximum ocular-vergence speed to maximum target-vergence speed were not systematically different between the two conditions in

which the target moved. During movement of the upper torso, the ratio was closer to unity. Thus the best match between the maximum speeds of ocular and target vergence was usually reached when the subject moved his upper torso towards and away from the stationary target. The distribution of the *mean* speeds (figure 4), averaged over the whole duration of movement, however, does not reveal any systematic difference in ocular vergence speeds as a function of the way in which the distance of the target was changed.

Differences in latency

Although the overall differences in ocular vergence speed between the three stimulus conditions were not very systematic, there were very consistent differences in the timing of ocular vergence relative to changes in target vergence. Delays between the onsets of changes in target vergence and changes in ocular vergence were computed only for the trials with 'very fast' target changes because only the onsets of these fast movements could be determined accurately. For 'very fast' movements, the acceleration of these 'very fast' responses was so high that ocular vergence speed increased from zero to far above threshold within one sampling period. Delays in this condition could therefore be estimated with an accuracy of 8 ms (the duration of one sampling interval). A reliable estimate of delays was not feasible for the conditions in which slower changes were made in the distance of the target. This limitation was due not only to the relative increase in the noise level of the data but also to the relatively gradual onset inherent in human-generated target movements when they were made at less than maximal speed. Mean delays for the 'very fast' condition, averaged over convergent and divergent movements, are shown in table 2.

TABLE 2. MEAN DELAYS OF FOUR SUBJECTS IN THE THREE MOTION CONDITIONS DURING 'VERY FAST' CHANGES IN TARGET VERGENCE

(All values given in milliseconds. Negative values indicate that ocular vergence movements preceded changes in target distance.)

| subject | experimental condition | | |
|--------------|-------------------------|--------------------|-------------------------|
| | experimenter, manual | subject, manual | subject torso motion |
| A.M. | 133 ± 17 | -65 ± 51 | -10 ± 9 |
| H.C. | 114 ± 19 | -77 ± 63 | -4 ± 12 |
| J.S. | 127 ± 25 | -157 ± 124 | -5 ± 15 |
| R.D. | 127 ± 29 | -76 ± 37 | -3 ± 7 |
| overall | | | |
| means ± s.d. | 125 ± 7 | -94 ± 37 | -5 ± 3 |

These delays are the means of at least 16 changes in the distance of the target. The delays were very similar in all subjects when the target was moved by the experimenter. The grand mean of 125 ms is considerably shorter (22%) than the 160 ms delay reported by Rashbass & Westheimer (1961) for vergence responses to stepwise changes in disparity. When the target distance was changed manually by the subject, the ocular vergence response started, on average, 94 ms *before* the onset of target movement. In all subjects divergence tended to have a shorter latency than convergence. This difference, which was most pronounced in subject

J.S., caused him to have an exceptionally large standard deviation (almost twice as large as the next most variable subject). When target distance was changed as a result of movements of the upper torso, ocular and target vergence changed almost synchronously. Convergent movements were very closely synchronized, whereas divergent movements tended to start slightly prematurely.

Differences in accuracy

The differences in timing of ocular-vergence responses in the three motion conditions had great consequences for the vergence error observed while the distance to the target changed 'fast' and 'very fast'. This can be seen clearly in graphs, plotting ocular-vergence position against target-vergence position (figure 6). If ocular vergence tracked target vergence perfectly, the curves plotted in fig. 6 would follow the dashed, diagonal lines. Departures from these lines indicate vergence errors.

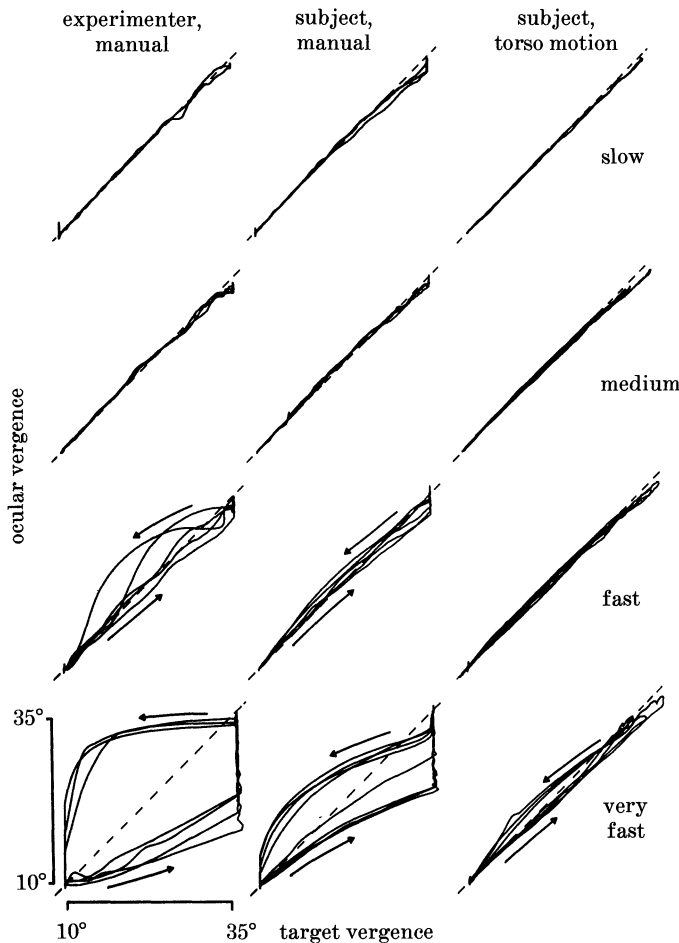


FIGURE 6. Typical relations between ocular-vergence angle and target-vergence angle of subject H.C. responding to slow (first row), medium (second row), fast (third row) and very fast (bottom row) changes in target distance. The three columns represent the three ways in which the distance of the target was varied. Diagonal, dashed lines represent completely accurate tracking.

Such departures were very small (less than 2°) for the 'slow' and 'medium' speed ranges (figure 6, first and second row). This illustrates the conclusion we drew from the data summarized in figure 5 that, for changes in target vergence at speeds up to about 20° s^{-1} , ocular vergence tracking was accurate to within 1° , irrespective of the way in which the distance of the target was changed. An intriguing motion-condition dependence was, however, found for the higher speeds. The comparison between conditions is particularly straightforward for the 'fast' speed range (figure 6, third row) because target vergence speeds were similar in all three motion conditions (see table 1). In the 'fast' condition tracking errors were very large when the target was moved by the experimenter, still prominent when the subject moved the target with his hand, whereas tracking was excellent when the distance of the target was varied at similar speeds by forward and backward motion of the subject's upper torso. These differences in tracking accuracy were even larger when motions were 'very fast' (figure 6, bottom row), but in this case errors were accentuated by differences in target-vergence speed among the three motion conditions. For the 'experimenter-generated, very fast' condition (figure 6, bottom left) errors were very large because the target had completed its entire trajectory before the ocular-vergence response had even started.

The vergence errors of up to 25° , occurring under the most demanding conditions (figure 6, bottom left), should have led to double vision of the target, at least temporarily. Double vision went unnoticed, possibly because such large disparities were present for only very short periods of time (less than 300 ms). Such transient, large disparities of an attended, moving object may occur so commonly in ordinary behaviour that subjects do not notice or remember diplopia, unless they are specifically alerted to attend to the phenomenon.

Figure 5, which plots average vergence error as a function of average speed of target vergence, shows that the differences observed among the three motion conditions were systematic. Comparison among the conditions is somewhat hampered by the fact that the fastest movements of the upper torso were never as fast as the fastest manual movements of the target. Some clear tendencies, however, can be seen. The errors when the experimenter moved the target (squares) tend to be larger than when the subject used his hand to move the target (diamonds). This is particularly clear for the highest two target vergence speeds, which were of similar magnitude for three of the four subjects. Furthermore, errors induced by changing the target distance by moving the upper torso (triangles) were lower for each of the four subjects at each target vergence speed.

Ocular vergence responses to targets imagined in darkness

The absence of delay, and even more compelling, the frequency with which changes in ocular vergence *preceded* changes in the distance of the target (delays were negative) show that these responses cannot be described adequately by a linear system model of the vergence subsystem, particularly in that these predictive responses did not require practice which would allow the vergence subsystem an opportunity to 'adapt' or to 'learn' how to predict its response. This point has been made, and supported empirically, before with respect to other oculomotor subsystems, notably smooth pursuit and saccades (Kowler & Steinman

1979*a, b*; Kowler *et al.* 1984*a*; Kowler & McKee 1987; Pavel 1989; Steinman 1986; Zingale & Kowler 1987).

Once it was clear that the vergence response could precede the change in the distance of the target, the question arose as to whether visual cues to depth were necessary for making ocular vergence responses. This question was answered by attempting binocular fixation of an imagined target moving back and forth in darkness either by holding the head still and having the subject move the imagined target back and forth by moving his arm, or by keeping the imagined target stationary and having the subject move his upper torso back and forth. In short, we redid the experiments in which the subject controlled the distance of the target under conditions in which he could not see where the target was, and could therefore only use signals to or from his torso or arm to drive his vergence subsystem.

Only two of the four subjects produced any ocular vergence responses while they fixated an imagined target whose distance was changed by moving their arm. Furthermore, these responses were poorly related to their arm movements with respect to speed, timing and amplitude. These results are rather similar to smooth pursuit studied under analogous conditions (Steinbach & Held 1968). These authors reported that commands sent to the arm could initiate smooth-pursuit-like eye movements in the absence of visual stimulation, but it is important to note that their effects, like ours, were ephemeral, idiosyncratic and very different from the responses made when the oculotor subsystem is provided with natural visual stimulation. Similar differences were reported between real smooth pursuit of a moving visual stimulus and imitations of smooth pursuit attempted with visible, but stabilized, stimuli (Cushman *et al.* 1984). Here, retinal slip, the natural input for smooth pursuit, was not available and only limited, idiosyncratic smooth eye movements were observed.

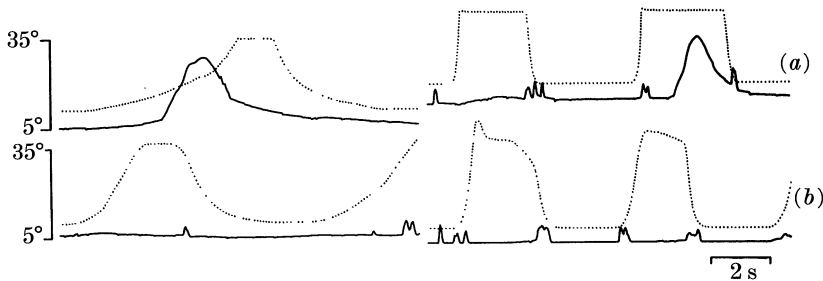


FIGURE 7. Ocular vergence responses (solid lines) of subject J.S. attempting to track imagined changes in target vergence (dotted lines) in darkness. The left panels show 'slow' movements and the right panels 'fast' movements. (a) Target moved by the subject; (b) changes in target distance induced by movements of the upper torso.

None of our subjects made any smooth ocular vergence responses that resembled the normal ocular vergence responses they made with visible targets, when they moved their upper torsos in darkness. These movements, which were often associated with blinks, did not bear any relation to the changing position of their heads relative to the imagined position of the stationary target (see Collewijn *et al.*

(1985) for the binocular eye movement pattern during blinks). Taken together, the results of the experiments done in darkness show that visual cues to depth are required for *effective* ocular vergence responses. The ocular vergence responses that can be initiated in the absence of good visual cues to depth are very limited in scope and quality, at least when they are examined before explicit training and when feedback as to their effectiveness was not provided to the subjects.

DISCUSSION

Ocular vergence movements associated with target motion

The ocular vergence responses, under all conditions studied in the present experiments, were superior to previous reports of ocular-vergence responses induced by disparity and/or blur. Our delays were shorter (the vergence responses often led the change in the distance of the target), our vergence speeds were much higher and the range of retinal disparity reduced by vergence responses was almost three times larger than disparities reduced in previous studies. Retinal disparity, which has been regarded as the most powerful driver of ocular vergence, has been reported to induce vergence responses with delays ranging from 160 to 240 ms. The maximum speed of ocular vergence driven by disparity in this prior work, however, was only about 20° s^{-1} when disparity was 5° (Erkelens 1987; Rashbass & Westheimer 1961). Even very large stereograms ($30^\circ \times 30^\circ$), which induced 'fast' (20° s^{-1}) ocular vergence responses with small disparities, no longer did so when disparities exceeded 10° (Erkelens 1987). Our vergence speeds reached up to about 100° s^{-1} and disparities as large as 25° were reduced.

The most likely reason for the drastic differences in results between our and previous experiments was the opportunity we gave our subjects to use the full repertoire of binocular and monocular cues to the depth of the target relative to themselves and to other objects and frames in the visual scene to initiate and guide their vergence responses.

In previous experiments, vergence was investigated by presenting, in an otherwise darkened room, targets whose disparity and/or blur was manipulated by the experimenter. Under such unnaturally reduced conditions, the perceived depth of the target would be, at best, uncertain, forcing the vergence subsystem to use the disparity and/or blur to maintain normal fused binocular vision; no other cues were available. Implicit in this kind of reduced-cue experiment is the notion that ocular-vergence responses to visual stimuli are controlled reflexively by properties of the stimulus. This notion seemed plausible because such ocular-vergence responses could not be suppressed under such unnatural stimulating conditions. The subject could not choose to attend to another feature in the visual scene; there were no other features that would permit him to maintain vergence at some other value in the presence of the blur and/or disparity provided by the experimenter. The vergence subsystem is not necessarily driven reflexively, but it can be made to appear to be so if the subject is not given the option of selecting alternative properties of the visual scene. It is precisely by means of stimulus selection that voluntary control operates in the oculomotor system. This point was first made

clearly, and supported empirically, by Kowler *et al.* (1984*b*) in an experiment in which two highly experienced eye movement subjects were asked either (1) to use smooth eye movements to maintain fixation (use 'slow control', Steinman *et al.* (1973)) on a full field of randomly positioned stationary dots that were superimposed on a full field of identical moving dots, or (2) to pursue the moving dots smoothly while ignoring the superimposed stationary dots. If one or the other field had been absent, smooth eye movements would have tracked the full field of moving dots or would have been relatively immobile on the full field of stationary dots. Neither of these responses, smoothly pursuing or staying in place, could have been suppressed voluntarily and it would have been plausible, but incorrect, to claim that smooth pursuit and slow control were reflexive responses to stimulus properties. The simultaneous presence of alternative stimulus configurations, however, allowed the subject to attend to either configuration almost exclusively. Once the choice was made by the subject, the smooth pursuit or slow control subsystems responded automatically to the retinal slip velocity of either the moving or the stationary configuration. These automatic reflexive responses were either effective smooth pursuit or effective slow control, depending on the configuration selected voluntarily by the subject. The reflexes, which came into play in this situation, were independent of the subject's perceptions or awareness of his actual oculomotor system responses. For example, the configuration of stationary dots were perceived as moving in the opposite direction to the configuration of moving dots ('induced' movement), but slow control velocity was almost zero once the subject chose the stationary field. He perceived himself as tracking the relatively slow induced movement of this stationary field while his eye was actually almost standing still. In other words, his reflexive slow control motor response reflected the true retinal slip velocity of the selected input configuration despite the illusory perceived motion of the objectively stationary field. Kowler *et al.* (1984*b*, p. 1796), based on these and a number of other observations, concluded that 'information about the configuration of the target is provided to the smooth oculomotor subsystem by means of voluntary processes, whereas information about the location or motion of the target is processed independently by the smooth oculomotor subsystem by means of mechanisms not susceptible to voluntary control'.

We believe that our study of natural vergence responses extend the conclusions reached by Kowler *et al.* (1984*b*) about the operation of the slow control and smooth pursuit subsystems to the operation of the vergence subsystem. Previous studies of vergence had used conditions that precluded voluntary selection (only one or another vergence reflex could operate). This methodology had led previous investigators to a false impression of the reflexive nature of the vergence subsystem. It also led them to underestimate the effectiveness of the vergence subsystem as it is used in the structured visual environment in which we normally function. In such an environment there is usually a rich variety of objects and cues to depth. When the subject voluntarily chooses to attend to one or another of these objects, its position in depth is provided to the vergence subsystem through these cues. Once a choice is made (possibly a target object suggested by an

experimenter), vergence subsystem reflexes operate automatically so as to produce vergence responses appropriate for binocular fixation at the depth plane occupied by the chosen object.

The visual significance of vergence-tracking errors

Our experiments give no indication of the visual consequences of the different vergence-tracking errors we observed. Diplopia was not noticed in any of our conditions, as would have been expected from previous reports of vision in the presence of natural binocular retinal image motion (cf. Steinman *et al.* 1985). Our observations are consistent with the earlier work on natural retinal-image motion in that they also suggest that oculomotor vergence subsystem performance, when studied under rather natural conditions, is more than adequate to maintain normal, fused binocular vision even when, as in the present case, the distance of the target from the subject's eye changed rapidly. In previous work with natural retinal-image motion, we had induced rapid and large changes in vergence by oscillating the head about a vertical axis while keeping a binocularly viewed distant landscape, a stereoacuity target or a random-dot stereogram at a fixed distance or at a fixed target disparity. Vergence errors during head oscillations seldom exceeded 2° . Errors were, however, frequently well over 1° : a very large value next to traditional values given for Panum's fusional area. The tolerance of the visual system to overall, absolute retinal disparities up to 2° is further corroborated by experiments in which the half images of random-dot stereograms were deliberately moved out of correspondence (Fender & Julesz 1967; Erkelens & Collewijn 1985 *a, b*).

The present work is a major extension of the earlier finding, however. It is completely new in that it is the first study of vergence rather than to employ natural binocular stimulation. Here, we looked at the relative effectiveness of the vergence subsystem when challenged with the changing of the cues to depths that are normally used to initiate and guide vergence tracking. In the earlier work, we had noted that vergence instabilities, which were produced by failures of Hering's law during head oscillations, occurred and that these vergence instabilities had negligible effects on important properties of binocular vision. This second conclusion was based on psychophysical experiments explicitly designed to examine visual processing in the presence of natural binocular retinal-image motion. At present, we know much less about the visual consequences of the vergence-tracking errors observed in these experiments than we know now about the visual effects of failures of Hering's law in the earlier head-oscillation experiments. The subjects did not report being bothered by diplopia, but the extent to which vergence-tracking errors of the magnitude observed in the present experiments affected more subtle aspects of their binocular vision will have to be determined in subsequent experiments in which psychophysical threshold measurements are made concurrently with activation of the vergence subsystem. At present, we only know that the vigorous vergence responses we observed had a sufficient dynamic range and were timely enough in all of our conditions to give the subjective impression of normal binocular vision when the target changed its depth with respect to the subject. This observation, which is based entirely on informal subjective reports,

might lose much of its generality and significance when the relevant thresholds are measured in concurrent psychophysical experiments.

This is a very real possibility because the dynamic inaccuracies in the present experiments are not identical to those in the previous experiments on the tolerance for disparity, cited above. The earlier work related to overall, *absolute* disparities between the complete retinal images. In the present experiments in which the target was moved manually, changes in *relative* disparity between the target and its background were produced. Our condition in which the subject moved his upper torso was more similar to the earlier work because it affected the overall disparity of target as well as of its background. However, in the present experiment this effect was compounded by the addition of optic-flow phenomena caused by moving the subject. (For extensive reviews of the significance of absolute and relative disparity for vergence and stereopsis see Collewijn & Erkelens (1989) and Collewijn *et al.* (1989).)

We are cautiously optimistic despite the concerns, however, that we will, once again, find that binocular visual processing fares unexpectedly well in the presence of relatively large errors during vergence tracking. Our optimism is based entirely on our previous work where subsequent psychophysical threshold measurements have confirmed informal subjective reports of normal vision despite appreciable retinal-image motion during head oscillations (Steinman *et al.* 1985).

The origin of vergence-tracking errors

Our experimental conditions differed in ways that could be expected to make vergence tracking more or less difficult. Difficulty, in all of our conditions, was varied by varying the speed of target vergence from 'slow' to 'very fast'. As expected, increasing target-vergence speed increased the difficulty of the tracking task and tracking error tended to increase, regardless of the means used to change the target's position in depth. These effects were modest, however, and it was only when the target moved faster than about 40° s^{-1} that average tracking errors began to exceed 2° consistently (see figure 5). We pointed out in the previous section that the visual significance of these tracking errors must be determined in future psychophysical threshold experiments. It seems desirable, however, to discuss the origin of the striking differences in tracking errors among our three motion conditions now, despite the fact that knowing the visual consequences of these tracking errors might allow us to provide more complete explanations.

The relatively poor performance observed when the experimenter moved the target was not surprising because the effectiveness of the subject's tracking depended entirely on his ability to anticipate motor responses produced by the experimenter (an external causal agent), and/or to attend to or to anticipate changes in the visual cues to depth caused by the experimenter. When the experimenter moved the target 'very fast', the subject's ocular vergence responses lagged, on average, about 125 ms behind changes in target vergence and they were, on average, too slow by about 36% (figure 4). The subject's relative uncertainty about the future position of the target, uncertainty that is inescapable when the experimenter moves the target, can be expected, simply on commonsense grounds, to cause relatively poor vergence-tracking accuracy. The importance of the

certainty of a subject's expectations about future target motion during oculomotor tracking can be supported, however, more directly than by appealing to common sense. Subjective certainty has been shown to be an important determinant of oculomotor performance in experiments on smooth pursuit (Kowler & Steinman 1981). So, the relatively large tracking errors observed when the subject depended on the experimenter's manipulations of the target's position in depth do not seem to be problematical. Performance should be relatively poor. It is important, however, to remember that it was only when the experimenter moved the target 'fast' or 'very fast' that these errors became appreciably larger than the errors observed when the subject controlled the target's position in depth.

The very different tracking errors observed when the subject, rather than the experimenter, used his arm to move the target are harder to explain. Here, the subject's ocular vergence responses *preceded* changes in target vergence by 95 ms, on average, when he moved the target 'very fast'. The speed of these ocular vergence responses was, on average, about 39% too slow, the same magnitude of speed error as when the experimenter moved the target. Why did the subject's ocular-vergence responses lead the changes in target vergence by almost as much as he lagged behind the changes of target vergence when the experimenter moved the target? A simple, mechanical and, therefore, potentially attractive possibility would be that commands to the arm to move the target and commands to the vergence subsystem to converge or to diverge to the expected future target's position in depth were sent at the same time. Possibly, the ocular-vergence changes preceded the target-vergence changes because of differences in neural and/or inertial characteristics of the oculomotor and arm motor systems. In other words, the subject was not actually attempting to track changes of the target's position in depth, at least not when he was required to move it 'fast' or 'very fast'. Rather, he was trying to coordinate the placement of the target with his binocular direction of his gaze so as to make them coincident at the predicted future target position. He was foiled in this attempt because his arm could not move in synchrony with his eyes when the commands to move both were issued simultaneously. This kind of interpretation implies that the tracking errors in timing and speed were not, or could not, be used effectively by the vergence subsystem, at least not before extensive practice with the specific task. It is possible that these tracking errors were not used to 'improve' performance because they did not have consequences for binocular vision, a point emphasized earlier.

There were even more striking differences in performance when the upper torso was moved rapidly back and forth to change the target's position in depth under instruction to move 'fast' or 'very fast'. Even these rapid movements of the upper torso permitted almost perfectly synchronized vergence tracking. Leads were, on average, only about 5 ms in the 'very fast' condition (about equal to our error of measurement of delay) and ocular vergence error was, on average, much smaller than in the other conditions. We shall rule out a simple mechanical explanation for the difference in results between the voluntary torso and arm moving conditions before considering other reasons for the differences observed.

When the upper torso moves back and forth, the otoliths could provide 'feed-forward signals' (i.e. signals preceding vergence changes), which could be used by

the vergence subsystem. The fact that ocular vergence responses did not occur when the head moved back and forth in darkness argues against such a reflexive contribution from the otoliths. There is an additional reason for ruling out signals from the otoliths, namely that the relation between the amount of vergence change required and signals generated by the otoliths, when the upper torso moves back and forth, cannot be signalled by the otoliths. A reflex utilizing signals from the otoliths to control ocular vergence responses would require near perfect monitoring of the current state of vergence by some inflow or outflow mechanism. Taken together, the otoliths do not seem to provide a likely explanation for the almost error-free vergence tracking observed when the upper torso moved back and forth.

Reasons for relatively accurate vergence tracking, when the subject moved his upper torso rather than his arm, will be considered now that signals from the otoliths have been discounted. There were three differences between these conditions that might have influenced performance differentially. Their relative importance cannot be established firmly without additional experiments, but their nature can be stated. First, target vergence speeds tended to be lower when the torso moved back and forth than when the arm moved the target back and forth, particularly in the 'fast' and 'very fast' condition. It is easier to track slower changes of target vergence. Second, when the target was moved back and forth manually, stops were provided to delimit the exact range of motion. The lever carrying the target hit these stops and introduced high-velocity transients into the target's trajectory (see figure 3). These transients might have perturbed the vergence subsystem. Third, moving the target back and forth by moving the arm changed *both* subject-relative and object-relative visual cues to depth simultaneously. In other words, the target's position in depth relative to other objects and frames in the visual scene changed as the target's position in depth relative to the subject also changed. Obtaining accurate information about exactly where the target was at any given instant required sorting through more information than was required when the upper torso moved back and forth. Depth cues from the target changed relative to depth cues from other objects and frames in the visual scene. The depth cues from these non-target objects (e.g. their size, blur and disparity) had to be excluded as much as possible by the subject as inputs to his vergence subsystem reflexes, much as the full field of moving or stationary dots had to be excluded as inputs to the smooth pursuit or slow control subsystem reflexes in the experiments on selective attention described earlier (Knowler *et al.* 1984*b*).

The demands made on the subject's ability to attend selectively to the target were reduced when the subject moved his upper torso while the target remained stationary. In this condition, the target maintained its relation to other objects and frames in the visual scene. Therefore, only subject-relative information was changing, and only this information had to be processed when the target's position in depth was changed by moving the upper torso. All visual objects and frames maintained their relative positions in depth with respect to each other in the physical world. They all provided information about the position of the subject's head relative to the visual scene that contained the target. This information remained internally consistent as the subject moved. Moving the upper torso back

and forth with respect to stationary objects in the visual scene is probably the simplest demand that can be placed on the ocular vergence subsystem. Even rabbits have been reported to change vergence consistently under such conditions (Zuidam & Collewijn 1979). It is not therefore surprising that the most accurate performance was observed in this condition.

Implications for vergence in other natural situations

We have shown that the vergence subsystem is as capable of timely and fast responses as the smooth pursuit or saccadic subsystems when the vergence subsystem is provided with its natural input, namely an environment containing a large number of effective cues to the depth of the objects contained within it. We also found compelling evidence for the fact that the vergence subsystem is subject to important voluntary influences, which, like the other oculomotor subsystems, take over control as soon as the subject attends selectively to one rather than to another property of potential visual input. The importance of voluntary control was demonstrated in the vergence subsystem in the same manner that it has been demonstrated in other oculomotor subsystems, that is by the frequency with which the vergence response preceded or coincided with changes in the relevant property of the input (the current distance of the selected target for vergence).

In these experiments, we demonstrated these properties by asking the subject to fixate a selected target object binocularly while its position in depth was varied by moving the target or by keeping the target stationary and moving the upper torso. Responses covered a very wide dynamic range, were very fast and often led changes in the position of the target. The vergence subsystem is often called upon to act rapidly and accurately over a wide range of disparities in other, rather different, natural settings. Specifically, human beings commonly fixate near, far and intermediate objects that are located on and also off to the side of the median plane. In the last case version, as well as vergence, eye movements are necessary to establish accurate binocular fixation. Often all objects, including ourselves, are stationary and the vergence changes are made entirely by shifting attention from one to another object, each located at a different depth plane. Does vergence work as well in these natural situations as we have seen it work when the attended target object moves with respect to ourselves? In the accompanying paper we shall show that it does when the stationary targets are confined to the median plane and that vergence saccades take on considerable importance when the attended target objects are displaced laterally as well as in depth (Erkelens *et al.* 1989).

This research was supported partly by the Foundation for Medical Research MEDIGON (The Netherlands) (grant no. 900-550-092), by NIH-NEI grant no. EY-04647 (U.S.A.), and partly by the Department of Psychology, University of Maryland. We thank Dr Robert Dooling and Dr Albert J. Martins for serving as subjects.

REFERENCES

- Alpern, M. & Ellen, P. 1956 A quantitative analysis of the horizontal movements of the eyes in the experiments of Johannes Muller. II. Effect of variation in target separation. *Am. J. Ophthalm.* **42**, 296–303.
- Collewijn, H. 1977 Eye and head movements in freely moving rabbits. *J. Physiol.* **266**, 471–498.
- Collewijn, H. & Erkelens, C. J. 1989 Binocular eye movements and the perception of depth. In *Reviews of oculomotor research*, vol. 4 (*Eye movements and their role in visual and cognitive processes*) (ed. E. Kowler). Amsterdam: Elsevier. (In the press.)
- Collewijn, H., Martins, A. J. & Steinman, R. M. 1981 Natural retinal image motion: origin and change. *Ann. N.Y. Acad. Sci.* **374**, 312–329.
- Collewijn, H., Martins, A. J. & Steinman, R. M. 1983 Compensatory eye movements during active and passive head movements: fast adaptation to changes in visual magnification. *J. Physiol., Lond.* **340**, 259–286.
- Collewijn, H., Steinman, R. M., Erkelens, C. J. & Regan, D. 1989 Binocular fusion, stereopsis and stereoacuity with a moving head. In *Vision and visual dysfunction*, vol. 10 A (*Binocular vision*) (ed. D. Regan). London: MacMillan. (In the press.)
- Collewijn, H., Van der Mark, F. & Jansen, T. C. 1975 Precise recording of human eye movements. *Vision Res.* **15**, 447–450.
- Collewijn, H., Van der Steen, J. & Steinman, R. M. 1985 Human eye movements associated with blinks and prolonged eyelid closure. *J. Neurophysiol.* **54**, 11–27.
- Cushman, W. B., Tangney, J. F., Steinman, R. M. & Ferguson, J. L. 1984 Characteristics of smooth eye movements with stabilized targets. *Vision Res.* **24**, 1003–1009.
- Erkelens, C. J. 1987 Adaptation of ocular vergence to stimulation with large disparities. *Expl Brain Res.* **66**, 507–516.
- Erkelens, C. J. & Collewijn, H. 1985a Motion perception during dichoptic viewing of moving random-dot stereograms. *Vision Res.* **25**, 583–588.
- Erkelens, C. J. & Collewijn, H. 1985b Eye movements and stereopsis during dichoptic viewing of moving random-dot stereograms. *Vision Res.* **25**, 1689–1700.
- Erkelens, C. J. & Regan, D. 1986 Human ocular vergence movements induced by changing size and disparity. *J. Physiol., Lond.* **379**, 145–169.
- Erkelens, C. J., Collewijn, H. & Steinman, R. M. 1989 Ocular vergence under natural conditions. II. Gaze shifts between real targets differing in distance and direction. *Proc. R. Soc. London. B* **236**, 441–465. (Following paper.)
- Fender, D. & Julesz, B. 1967 Extension of Panum's fusional area in binocularly stabilized vision. *J. opt. Soc. Am.* **57**, 819–830.
- Kowler, E. & McKee, S. P. 1987 Sensitivity of smooth eye movement to small differences in target velocity. *Vision Res.* **27**, 993–1015.
- Kowler, E. & Steinman, R. M. 1979a The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Res.* **19**, 619–632.
- Kowler, E. & Steinman, R. M. 1979b The effect of expectations on slow oculomotor control. II. Single target displacements. *Vision Res.* **19**, 633–646.
- Kowler, E. & Steinman, R. M. 1981 The effect of expectations on slow oculomotor control. III. Guessing unpredictable target displacements. *Vision Res.* **21**, 191–203.
- Kowler, E., Martins, A. J. & Pavel, M. 1984a The effect of expectations on slow oculomotor control. IV. Anticipatory smooth eye movements depend on prior target motions. *Vision Res.* **24**, 197–210.
- Kowler, E., Van der Steen, J., Tamminga, E. P. & Collewijn, H. 1984b Voluntary selection of the target for smooth eye movement in the presence of superimposed, full-field stationary and moving stimuli. *Vision Res.* **24**, 1789–1798.
- Pavel, M. 1989 Cognitive models of predictive tracking. In *Reviews of oculomotor research*, vol. 4 (*Eye movements and their role in visual and cognitive processes*) (ed. E. Kowler). Amsterdam: Elsevier. (In the press.)
- Rashbass, C. 1981 Reflexions on the control of vergence. In *Models of oculomotor behavior and control* (ed. B. L. Zuber), pp. 139–148. Boca Raton: CRC Press.
- Rashbass, C. & Westheimer, G. 1961 Disjunctive eye movements. *J. Physiol., Lond.* **159**, 339–360.

- Skavenski, A. A., Hansen, R. M., Steinman, R. M. & Winterson, B. J. 1979 Quality of retinal image stabilization during small natural and artificial body rotations in man. *Vision Res.* **19**, 675–683.
- Steinbach, M. J. & Held, R. 1968 Eye tracking of observer-generated target movement. *Science, Wash.* **161**, 187–188.
- Steinman, R. M. 1986 The need for an eclectic, rather than systems, approach to the study of the primate oculomotor system. *Vision Res.* **26**, 101–112.
- Steinman, R. M. & Collewijn, H. 1980 Binocular retinal image motion during active head rotation. *Vision Res.* **20**, 415–429.
- Steinman, R. M., Haddad, G. M., Skavenski, A. A. & Wyman, D. 1973 Miniature eye movements. *Science, Wash.* **181**, 810–819.
- Steinman, R. M., Levinson, J. Z., Collewijn, H. & Van der Steen, J. 1985 Vision in the presence of known natural retinal image motion. *J. opt. Soc. Am. A* **2**, 226–233.
- Westheimer, G. & Mitchell, G. 1956 Eye movement responses to convergence stimuli. *Am. med. Ass. Archs. Ophthalmol.* **55**, 848–856.
- Zingale, C. M. & Kowler, E. 1987 Planning sequences of saccades. *Vision Res.* **27**, 1327–1341.
- Zuidam, I. & Collewijn, H. 1979 Vergence eye movements of the rabbit in visuomotor behavior. *Vision Res.* **19**, 185–194.