

BINOCULAR CO-ORDINATION OF HUMAN HORIZONTAL SACCADIC EYE MOVEMENTS

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SUMMARY

1. The binocular co-ordination of human horizontal saccades was analysed for the first time systematically over the full oculomotor range with a precise and accurate scleral sensor coil technique. Effects of amplitude (1.25–80 deg), direction (adduction *vs.* abduction and centrifugal *vs.* centripetal) and eccentricity (symmetrical about primary or between primary and secondary positions) were systematically investigated in three subjects).

2. To minimize extraneous effects of stimulus presentation on the programming of saccades, subjects were instructed to voluntarily change their gaze between two continuously visible targets. These were positioned on an iso-vergence locus, and thus contained no stimulus for disjunctive eye movements.

3. Under these conditions the amplitudes of the primary saccades of the two eyes were remarkably accurate; undershooting of the target by about 0.5 deg (independent of amplitude in the range 10–70 deg) was typical. This finding contrasts with the undershooting by about 10% described in the literature as characteristic for other stimulus conditions.

4. Saccadic peak velocities saturated at a mean asymptotic level of 502 ± 32 (s.d.) deg/s for saccades of 40 deg and larger. The duration was linearly related to amplitude for saccades up to 50 deg; for saccades of larger sizes the duration increased progressively more steeply. Skewness values (acceleration time as a fraction of total saccadic duration) decreased from about 0.45 for saccades up to 10 deg to about 0.20 for saccades of 50 deg and larger.

5. Binocular saccades showed an abduction–adduction asymmetry and were not well yoked dynamically. The saccades of the abducting eye consistently had a larger size, a higher peak velocity, a shorter duration and were more skewed than the concomitant adducting saccades of the fellow eye. As a result, the eyes diverged transiently by as much as 3 deg during horizontal saccades.

6. Saccades also showed a marked centrifugal–centripetal asymmetry. Peak velocities of saccades towards the primary position were about 10% higher than peak velocities of corresponding centrifugal saccades.

7. These directional asymmetries were the main source of variability in the pool

of saccades. In comparison, intra- and intersubject variability was minor in our sample.

8. Post-saccadic drift consisted of a vergence and a version component. The vergence component of this drift was a continuation of the vergence movement occurring during saccades. The version component, generally smaller than the vergence component, was directed towards the target position. The result of post-saccadic drift was that the fovea of each eye was guided towards the target. The net post-saccadic drift of the abducting eye was smaller than that of the adducting eye, a result appropriate to reduce fixation errors remaining at saccadic offset.

9. A tight relationship between skewness and saccade duration was not found. For instance, velocity profiles of centrifugal saccades were more skewed than those of centripetal saccades whose duration was equal.

10. The main parameters of saccades were not different for binocular and monocular viewing; the degree of yoking, however, was decreased when the targets were viewed monocularly.

11. We conclude that binocular horizontal saccades between continuously visible stationary targets are accurate and highly reproducible within and between subjects. However, saccadic parameters are systematically affected not only by size, but also by direction and initial position.

INTRODUCTION

Human saccadic eye movements appear to be rather stereotyped behaviours, a fact which has encouraged attempts to characterize the saccadic waveform with a limited number of parameters. Ever since Westheimer (1954) found a tight relationship between peak velocity and amplitude of saccades these variables, together with duration, have become the main parameters used to describe saccades. The peak velocity *vs.* amplitude relation, sometimes called the 'main sequence' (Bahill, Clark & Stark, 1975), in general shows a linear increase of peak velocity as a function of saccade amplitude for relatively small saccades with a soft saturation of peak velocity for larger saccades. Normative data for horizontal saccades have been reported by Boghen, Troost, Daroff, Dell'Osso & Birkett (1974), Bahill *et al.* (1975) and Baloh, Sills, Kumley & Honrubia (1975). These existing data on the normal parameters of human saccades are not entirely satisfactory for a number of reasons: (1) there is large variability between investigators, between subjects and within subjects; (2) data for vertical saccades and for large saccades in any direction are scarce; (3) many data have been collected with stimulus conditions that are less likely to bring out normal saccadic behaviour; (4) there are virtually no reliable binocular recordings to assess the degree of yoking of the eyes. These four general limitations can be detailed as follows:

(1) Although the general shape of the peak velocity *vs.* amplitude relation does not differ much among several investigations, the actual values of the peak velocities and the level of saturation vary greatly. Peak velocities as high as 900 deg/s have been reported (Bahill, Brockenbrough & Troost, 1981) for saccades with a size of only 15 deg. Mean values of peak velocities given for larger data bases are much lower, but still show large differences. For instance, for 20 deg saccades Boghen *et al.* (1974) reported a mean maximum speed of about 375 deg/s; a mean value of about 420

deg/s can be derived from data presented by Baloh *et al.* (1975), while Bahill *et al.* (1981) found a mean maximum speed of 657 deg/s. One of the principal sources of this disagreement is undoubtedly the variety in methods of recording and data analysis. Bandwidth limitation in the recording of eye position and the derivation of eye velocity can lead to a serious underestimation of peak velocities (Bahill *et al.* 1981). But even in one laboratory, the variability between and within subjects appears to be large. Therefore, other sources of variability seem to be important. In addition to genuine intersubject variability, there may be many intrasubject sources of variability. One possible source is fatigue, considered as a main factor by Bahill & Stark (1975) although more recently denied by others (Schmidt, Abel, Dell'Osso & Daroff, 1979; Fuchs & Binder, 1983). Another possibility is a systematic dependence of saccadic parameters upon the direction (nasal or temporal, up or down, centrifugal or centripetal) or orientation of the saccade within the oculomotor range (symmetrical around the primary position, or within a peripheral sector of the range). There is ample, but conflicting, evidence that naso-temporal asymmetries affect the shape of horizontal saccades (Hyde, 1959; Cook, Stark & Zuber, 1966; Robinson, 1964; Fricker, 1971). Faster dynamics of centripetal than of centrifugal saccades have been mentioned by Frost & Pöppel (1976), Abel, Dell'Osso, Daroff & Parker (1979), Jürgens, Becker & Kornhuber (1981), and Inchingolo, Spanio & Bianchi (1987) and were very recently studied more systematically by Pelisson & Prablanc (1988). If such factors have systematic effects, one has to be cautious about pooling saccadic data into a single 'main sequence'.

In the present study we used an extremely accurate and precise scleral sensor coil technique, developed in the laboratory of one of the authors (R.S.), to systematically investigate effects of direction and location within the oculomotor range on saccadic parameters.

(2) As most recording techniques do not allow the reliable recording of either vertical saccades or very large saccades in any direction, there is a shortage of data on such eye movements. The scleral coil technique does not suffer from such limitations. Accordingly, target separations in the present study ranged up to 80 deg for horizontal saccades. Results for vertical saccades, ranging up to 70 deg, are reported in an accompanying paper (Collewijn, Erkelens & Steinman, 1988).

(3) Most natural saccades are made voluntarily between targets which are relatively fixed in space and more-or-less continuously visible among many other potential targets. Nevertheless, they have been typically studied as reflex events, elicited by jumping or suddenly appearing or disappearing targets. The importance of this distinction has been recently supported by an innovative study of Zingale & Kowler (1987), in which it was shown that saccades are programmed as part of an organized pattern of motor activity, and not merely as reactions to local sensory stimulation. Accordingly, we tried to approximate a more normal situation by lighting two light-emitting diodes (LEDs) within a single trial and instructing the subject to saccade between these LEDs at a non-stressful pace while they were seen against many other visual details in the room.

(4) An important issue in oculomotor research is the degree of yoking of the two eyes. Hering's law expresses a firm belief in the perfect conjugacy of the eye movements in the absence of a stimulus for vergence. Any nasal-temporal asymmetry would in principle violate this law. Although yoking is traditionally assumed, no

direct confirmation from accurate oculomotor recordings is available. Binocular eye movement recordings during free head movements have, however, demonstrated considerable disjunctive components in compensatory eye-in-head movements (Steinman & Collewijn, 1980; Steinman, Levinson, Collewijn & Van der Steen, 1985). Because the scleral coil technique is eminently suitable for use on both eyes simultaneously, we made binocular recordings in all experiments, using binocular vision routinely. Monocular vision (with one of the eyes covered) was occasionally used but all recordings were binocular.

An important consideration in studying the conjugacy of eye movements is to avoid any stimulation of vergence. In general, the angles subtended by two targets in space are unequal at the two eyes. If a target *F* is binocularly foveated, all other targets in the plane of regard, requiring yoked eye movements, lie on a circle through *F* and the centres of rotation of both eyes. We call this an 'iso-vergence circle'. This locus of equal vergence can be extended in the vertical dimension by rotating the iso-vergence circle around the baseline connecting the two centres of rotation, thus forming a toroid 'iso-vergence surface'. A family of such surfaces represents the different values of iso-vergence. For a convergence angle of zero (parallel visual axes) the surface becomes a flat and fronto-parallel plane at infinite distance. We carefully located our targets within a single iso-vergence surface. A short preliminary communication of the present results has been made (Collewijn, Erkelens & Steinman, 1987).

METHODS

Four subjects (including the authors) participated in the experiments. All had 20/20 visual acuity or better, without ($n = 2$) or with ($n = 2$) correction. None of them showed any ocular or oculomotor pathologies, but some refractive anomalies were present. Three of the subjects, an emmetropic and presbyopic male (R.S., age 60 years), a myopic male (C.E., age 36 years) wearing negative contact lenses, and a myopic and presbyopic male (H.C., age 51 years), normally wearing negative corrective spectacles, were experienced in oculomotor research. The other subject, an emmetropic male (R.D., age 35 years), had served only occasionally in such experiments. Subject H.C. did not wear any refractory correction for at least 3 h prior to an experiment.

The revolving magnetic field-sensor coil technique was used to record absolute horizontal and vertical 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, Martins & Steinman, 1981). Briefly, sensor coils were attached to the eyes and homogeneous magnetic fields rotating in the horizontal and sagittal planes (field frequencies: 976 and 3904 Hz) were generated around the subject. The phase of the alternating electric potentials induced by the fields in a sensor coil is linearly related to the latter's angular orientation. In the instrument used in the present experiments, generation of the field and phase detection of the induced signals were digitally controlled; special filtering techniques allowed perfect separation between signals induced by horizontal and vertical fields. The noise level was < 40 seconds of arc; linearity was better than 0.01% over 360 deg. Stability was better than 6 seconds of arc (for a fixed sensor coil) over periods from 1 s to 24 h. The maximum slewing speed of the digital output was 12000 deg/s. The instrument was not sensitive to linear displacements of the coil within the range occurring in our experiments. Coils embedded in a self-adhering silicone annulus as described by Collewijn, Van der Mark & Jansen (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 confirmed for the present experimental apparatus (Collewijn *et al.* 1981). Head movements were minimized by using bite boards with individually fitted dental impressions. During the experiments the room was dimly lit.

The visual targets consisted of forty-six LEDs arranged on the horizontal and vertical meridians of an iso-vergence surface (see Introduction). Specifically, targets were placed on a horizontal circle

with a diameter of 91.4 cm (3 ft) on which the centres of rotation of the eyes (assumed to be 13 mm posterior to the corneal plane) were also placed. Vertical targets were placed in the median plane on a circle with a radius of 91.4 cm, centred on the mid-point of the inter-ocular baseline. In the horizontal plane, angles α between the central fixation LED and a target LED (Fig. 1) measured 1.25, 2.5 and from 5 deg up to 40 deg with increments of 5 deg on either side of the central fixation point. In the median plane, angle β (Fig. 1) measured 1.25, 2.5 and from 5 deg up to 30 deg in the upward direction, and up to 40 deg downward also with increments of 5 deg. It should be noted that in general a locus of iso-vergence does not correspond to a locus of iso-distance (measured from the centre of the interocular baseline to the target), except at infinite distance.

Each experiment consisted of forty-eight trials in which the subject made saccadic eye movements between two LEDs at the pace of a metronome set at 52 beats/min. Each trial lasted 10 s. Trials were started by the subject who pushed a button after he had made a few saccades and felt that he had established a comfortable rhythm. During the trials the horizontal and vertical positions of the two eyes were sampled at 488 Hz. Only the two LEDs that served as targets were lit. Two classes of target positions were used: (1) the two LEDs were positioned symmetrically around the fixation point centred in the iso-vergence surface; (2) the centred fixation LED was lit in combination with any other LED in the periphery. Target class, target distance and target plane were ordered in a pseudo-random sequence. In the first experiment viewing was binocular. In the second experiment binocular viewing was interleaved with monocular viewing with either the left or right eye. The first experiment was replicated for three of the four subjects (the authors) on different days.

The stored samples represent the positions of the eyes relative to earth-fixed co-ordinates. Due to the principle of the instrument calibration of angular rotation was absolute and independent of the subject or the sensor coil used. Only standardization to zero position during fixation of the centred fixation LED was required. The accuracy of the instrument in determining the angles of the eyes was virtually perfect. In fact the noise level of 40 seconds of arc was almost completely caused by the limited number of discrete levels (sixteen bits) of the digital data, and equalled the bit-noise of the least-significant bit. Accordingly, velocities were simply calculated as the difference between two subsequent samples, divided by the sampling interval. No additional filtering, smoothing or window techniques were used. Accordingly, the bit-noise in the velocity signal was about 6 deg/s (40 seconds of arc/(1/488 s)). The effective bandwidth of both position and velocity was 244 Hz.

In the off-line analysis, saccade onset as well as saccade offset were detected by a velocity threshold of 15 deg/s in combination with a required minimum saccade duration of 15 ms. By using this criterion any saccades larger than 1 deg were reliably detected. Subjects attempted to refrain from making blinks during trials, lasting 10 s. Any blinks that occurred were detected by visual inspection of the position signals and removed from the data (see Collewyn, Van der Steen & Steinman, 1985, for the blink eye movement waveform observed with our recording technique).

Amplitude, maximum speed (the length of the peak-velocity vector), duration and skewness (acceleration period as a fraction of total saccade duration) of velocity profiles of saccades were computed from the position signals of the two eyes. These dependent variables were submitted to a statistical analysis program (SPSS^{*}). An analysis of variance was carried out on the data in which subject, target amplitude, measured eye, saccade direction and target location were the independent variables. Mean values and standard deviations of the dependent variables for specific combinations of independent variables were also computed. Results from the experiments in which targets were viewed binocularly as well as monocularly were treated as a separate data set in which the viewing eye was an additional independent variable. Mean velocity profiles of saccades averaged within a single combination of independent variables were compared between the two eyes. Variability of saccades was further investigated by inspection of the two-dimensional saccadic trajectories projected onto a fronto-parallel plane.

Post-saccadic drift was calculated for two successive intervals: (1) mean eye velocity was computed for a period of 100 ms after each saccade. This period started 20 ms after the end of each saccade in order to avoid contamination by the dynamic overshoot frequently associated with a saccade; (2) mean eye velocity was computed for a successive period of 200 ms starting 120 ms after the end of each saccade. Post-saccadic drift was calculated during the longer period to get an impression of its time course and duration. Any small corrective saccades occurring after the primary saccade within these periods were removed.

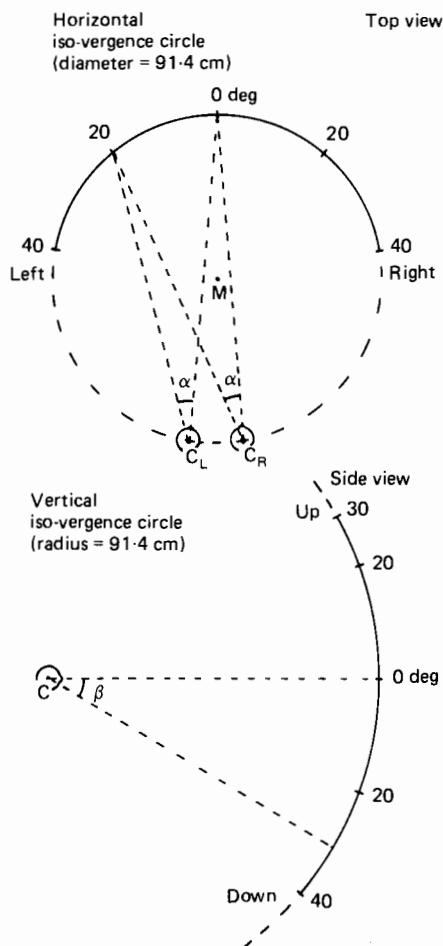


Fig. 1. Stimulus arrangement for horizontal (top) and vertical (bottom) saccades. For horizontal saccades the targets were placed on a circle with centre M and a diameter of 91.4 cm on which the centres of rotation of the eyes (C_L and C_R) were placed. The range of the target positions was 40 deg to each side of the central fixation point. For vertical saccades the targets were placed on a circle with a radius of 91.4 cm centred on the mid-point of the inter-ocular baseline (C). The target positions ranged from 30 deg upwards to 40 deg downwards.

RESULTS

Saccades between targets symmetrical about the primary position

Characteristics of binocular saccades

The subjects changed their fixation between the stationary targets by making saccades that covered the required distance accurately in most cases. In the instances when these primary saccades were followed by small corrective saccades, the corrective saccades were not analysed.

Families of typical position and velocity profiles of primary saccades with

amplitudes between 5 and 80 deg are shown in Fig. 2. The small standard deviations in the position, as well as in the velocity signals, indicate that the primary saccades between stationary targets were very reproducible. The velocity profiles show that acceleration, as well as peak velocity, increased with amplitude up to about 40 deg. For larger saccades the acceleration phases were very similar. Larger amplitudes were reached by prolongation of the deceleration phase which implies that the velocity profiles became very skewed.

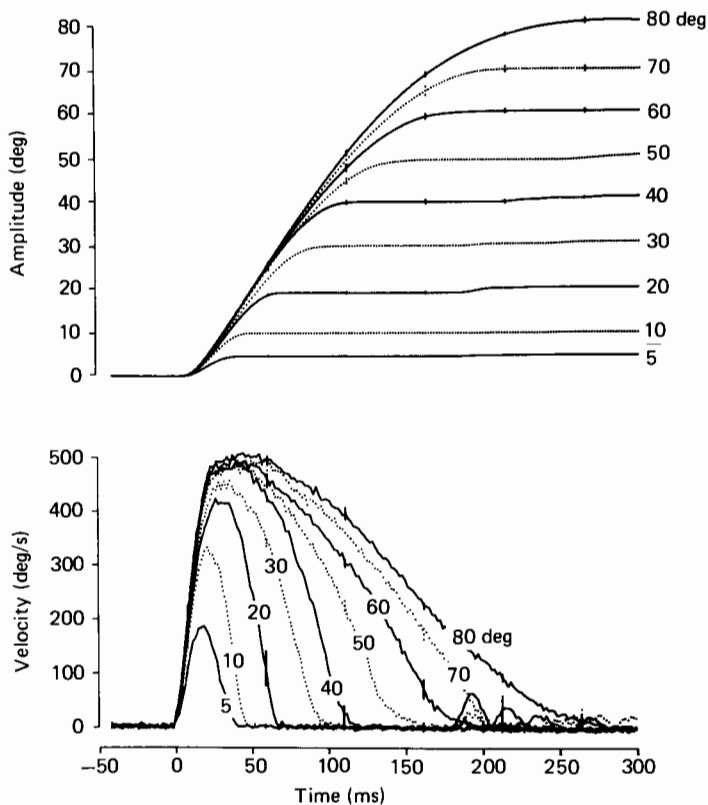


Fig. 2. A family of typical position (top) and velocity (bottom) profiles of horizontal saccades ranging from 5 to 80 deg. Each curve represents the average of four rightward saccades of subject R.S. made within the same 10 s trial; vertical bars indicate ± 1 s.d.

In the analysis, it turned out that the results for one subject (H.C.) differed markedly from those of the other three subjects. Subject H.C. normally wears corrective spectacles with anisometric corrections for the left and right eye. In another paper we will report that saccades of the two eyes can be differentially modified and become unequal in size by the wearing of anisometric spectacle corrections. The atypical performance of this subject was likely to reflect the presence of such modification even after leaving the spectacles off for 3 h before each recording session. We decided to exclude the data of this subject from the analysis of saccadic parameters for this reason.

The horizontal saccades made between stationary targets in the present paradigm

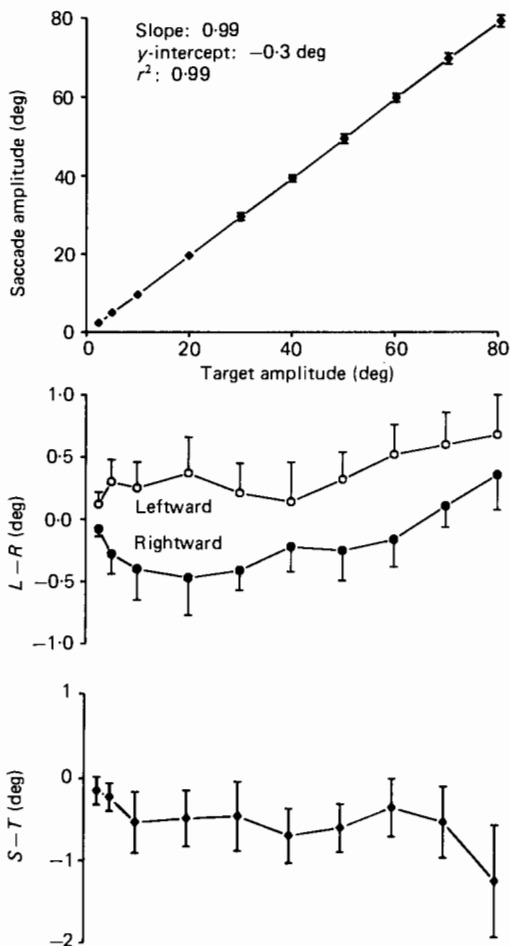


Fig. 3. Amplitudes of saccades (means of three subjects) made between targets located symmetrically about the central fixation point (upper panel). Data from the two eyes in the two horizontal directions have been pooled. Vertical bars indicate ± 1 s.d. The middle panel shows differences between saccade amplitudes (means of three subjects) of the left (*L*) and right (*R*) eye. \circ , leftward saccades; \bullet , rightward saccades. Vertical bars indicate 1 s.d. The lower panel shows differences between mean saccade amplitude (*S*) and target amplitude (*T*). Results presented in all figures were obtained from the same set of data.

were very accurate for small, as well as for large, amplitudes (Fig. 3). All subjects showed a slight undershoot for the primary saccade amplitude relative to the stimulus angle. The lower panel of Fig. 3 shows that the undershoot was independent of saccade amplitude between 10 and 70 deg. The mean undershoot was 0.5 deg in this range. The difference between the angles subtended by the two targets and the amplitudes of the primary saccades was less than 1 deg for 82% of all horizontal saccades. This finding contrasts with most previous descriptions in two important respects: (1) undershoot was considerably smaller than 10%; (2) undershoot was not a fixed percentage of target eccentricity.

There was no significant group difference between amplitudes of saccades made by the left or by the right eye. However, a marked effect of direction was found for saccades made simultaneously by the two eyes. Temporal saccades of one eye were significantly larger ($P < 0.01$) than the corresponding nasal saccades of the fellow eye for target distances up to 60 deg (Fig. 3, middle panel). For 70 and 80 deg saccades the left eye made slightly larger saccades than the right eye in two subjects, while left

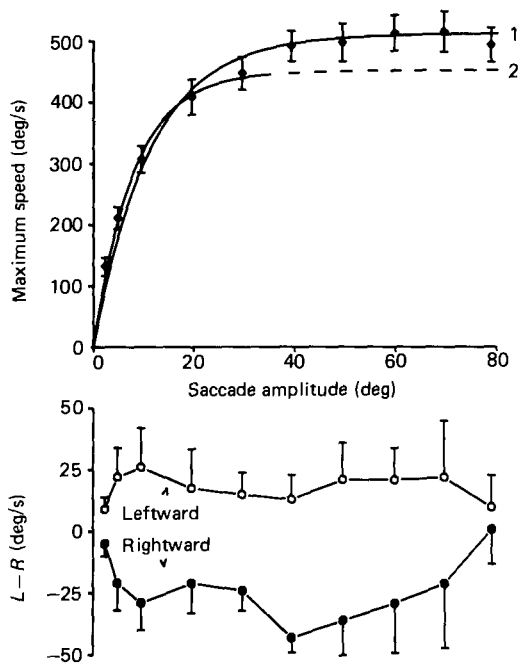


Fig. 4. Maximum speeds of saccades (means of three subjects) made between targets located symmetrically about the central fixation point (upper panel). Data from the two eyes in the two horizontal directions have been pooled. Vertical bars indicate ± 1 s.d. Curve 1 presents the best exponential fit of all data; curve 2 is the best exponential fit of data from saccades up to 30 deg. The lower panel shows differences between maximum speeds (means of three subjects) of the left (L) and right (R) eye. \circ , leftward saccades; \bullet , rightward saccades. Vertical bars indicate 1 s.d. Results presented in both figures were obtained from the same set of data.

and right eye saccades were equally large in the third subject. The difference observed between temporal and nasal saccades resulted in a relative divergence (decrease in convergence) of the eyes by an average of 0.3 deg at saccade offset. Thus, at the end of horizontal saccades the binocular fixation point did not lie on the isovergence circle through the target but on a circle with a larger diameter.

Figure 4 (upper panel) presents the mean maximum speed *vs.* amplitude relationship of horizontal saccades. This relationship was clearly non-linear for the measured amplitudes (2.5–80 deg). For amplitudes between 40 and 80 deg there was no significant difference ($P > 0.05$) between the mean maximum speeds. At these amplitudes, where the maximum speed was saturated, the mean level was

502 ± 32 (s.d.) deg/s. In view of this asymptotic behaviour for large amplitudes, the data were fitted with the following exponential function:

$$V_m = V_0[1 - \exp(-A/A_0)],$$

where V_m = maximum speed, A = saccade amplitude, and V_0 and A_0 are constants. V_0 expresses the asymptotic limit for the maximum speeds and A_0 indicates the

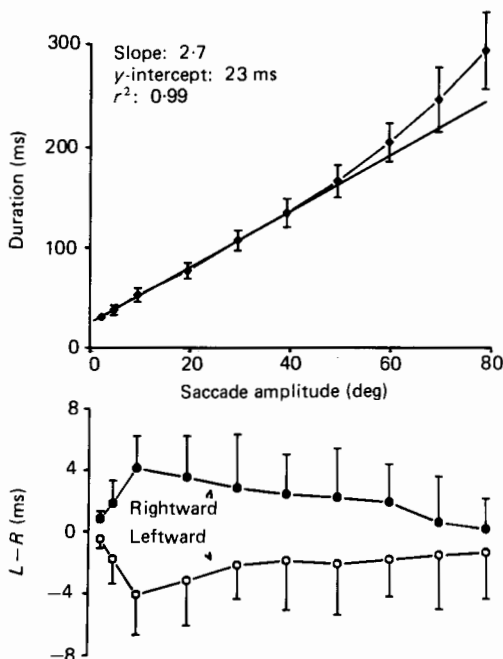


Fig. 5. Duration of saccades (means of three subjects) made between targets located symmetrically about the central fixation point (upper panel). Data from the two eyes in the two horizontal directions were pooled. Vertical bars indicate ± 1 s.d. The straight line represents a linear regression for saccades up to 50 deg (see text). The lower panel shows differences between saccade durations (means of three subjects) of the left (L) and right (R) eye. \circ , leftward saccades; \bullet , rightward saccades. Vertical bars indicate 1 s.d. Results presented in both figures were obtained from the same set of data.

saccade amplitude at which the maximum speed is 63% of V_0 . The fit of maximum-speed data of all saccade amplitudes was optimal for $V_0 = 520$ deg/s and $A_0 = 11.2$ deg. This function had a coefficient of determination (r^2) of 0.88. When, however, only data points for amplitudes up to 30 deg were taken into account, the best fit was achieved for $V_0 = 450$ deg/s and $A_0 = 7.9$ deg. These fits, which are shown in Fig. 4, indicate that extrapolation of V_0 on the basis of data for small amplitudes gives a poor estimate of the highest speed that can be reached during large saccades (assuming, of course, an exponential relation). The variability of maximum speeds among the subjects was surprisingly small. The main effects of subjects and eyes were not significant ($P > 0.05$) for amplitudes between 10 and 60 deg. A substantial part of the total variability was due to intrasubject differences between temporal and nasal saccades (Fig. 4, lower panel). The maximum speeds of binocular paired

saccades were about 20 deg/s higher for the abducting eye than for the adducting eye. This difference was highly significant ($P < 0.001$) for amplitudes up to 70 deg.

The relationship between duration and amplitude of horizontal saccades is shown in Fig. 5. For amplitudes up to 50 deg this relation was well described by the following linear function:

$$\text{duration} = 2.7 \times \text{amplitude} + 23 \text{ ms} \quad (r^2 = 0.99).$$

For saccades larger than 50 deg, saccade duration increased progressively more steeply as a function of amplitude. Similarly, there was a difference between the durations of binocular, paired saccades just as there was for amplitude and maximum speed. Temporal saccades of one eye lasted slightly shorter than the concomitant nasal saccades of the other eye. These differences were small (between 2 and 4 ms) but significant ($P < 0.01$) for saccades up to 60 deg.

Skewness, defined as the time between saccade onset and peak velocity (the acceleration period) as a fraction of the total saccade duration, was used as a fourth parameter for describing saccades. For example, a skewness of 0.5 means that the period of acceleration was as long as the period of deceleration. Mean values of saccadic skewness are shown in Fig. 6. The upper panel of this figure shows that horizontal saccades up to 10 deg had a rather symmetrical velocity profile. With amplitudes increasing from 10 to 50 deg saccades became progressively more skewed in such a way that the acceleration phase was shorter than the deceleration phase. An asymptotic value of about 0.20 was maintained in the range 50–80 deg. Skewness was also markedly different for temporal and nasal saccades. Saccades of the abducting eye were more skewed than the paired saccades of the adducting eye (Fig. 6, lower panel). This difference was highly significant ($P < 0.001$) for saccades between 10 and 70 deg. Once more, the main effects of subjects and eyes were not significant ($P > 0.05$).

In summary, when the eyes made horizontal saccades between stationary targets lying on an iso-vergence circle, these saccades were unequal in the two eyes with respect to four parameters. Saccades of the abducting eye were significantly larger in size, had higher maximum speeds, had a shorter duration, and were more skewed than the corresponding saccades of the adducting eye. These differences were large enough to be easily observed in the records of eye position and velocity. Typical examples of velocity and position profiles of binocular saccade pairs are shown in Fig. 7. This figure shows mean profiles of four horizontal saccades made in each direction between two targets (symmetrical about the mid-point) with a distance of 50 deg by the two eyes of one subject. The velocity profiles show that saccade onset occurred at the same time in the two eyes and that the abducting eye accelerated faster to its maximum speed than the adducting eye. Even though the acceleration phase of the abducting eye was shorter, this eye attained a higher maximum speed than the adducting eye. The systematically different velocity profiles of the two eyes introduced a disjunctive component as is shown in the vergence position traces. During the acceleration period the vergence angle changed in the divergent direction. The transient divergence reached its maximum when the velocities of the two eyes became equally large. This transient divergence was characteristic for all horizontal saccades and was observed at all amplitudes and in all subjects (including subject

H.C.). Angles between 1 and 3 deg were typical for the maximum change in vergence. From the moment the velocity of the adducting eye became larger than that of the abducting eye, vergence changed again but now in the convergent direction. This change of vergence continued even after saccade offset. At saccade offset the change in the convergent direction was insufficient to make up for the preceding movement

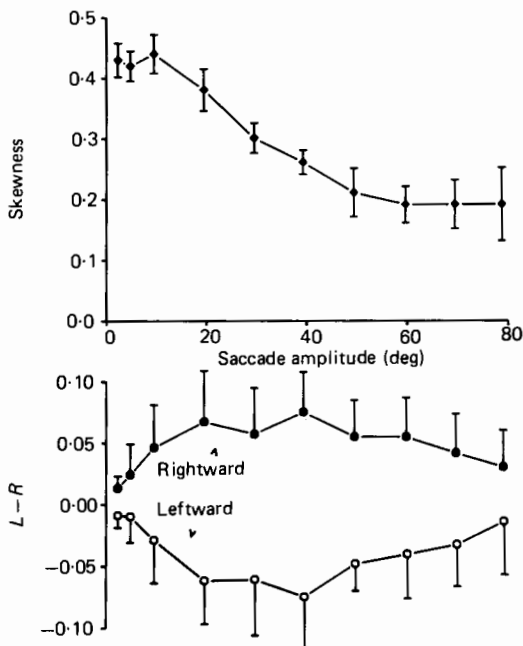


Fig. 6. Skewness of saccades (means of three subjects) made between targets located symmetrically about the central fixation point (upper panel). Data from the two eyes in the two horizontal directions have been pooled. Vertical bars indicate ± 1 s.d. The lower panel shows differences between skewness of saccades (means of three subjects) of the left (*L*) and right (*R*) eye. \circ , leftward saccades; \bullet , rightward saccades. Vertical bars indicate 1 s.d. Results presented in both figures were obtained from the same set of data.

in the divergent direction. There was still a net divergence, and thus a binocular fixation error of about 0.3 deg, in the divergent direction. This residual error was further reduced by the subsequent post-saccadic drift.

Post-saccadic drift

Version and vergence traces, such as those shown in Fig. 7, clearly indicated the presence of post-saccadic drift. The amount of such post-saccadic drift (calculated as the mean velocity during a period of 100 ms starting 20 ms after saccade offset) is shown in Fig. 8. Post-saccadic drift had both conjugate and disjunctive components. Vergence drifted in the convergent direction of all amplitudes of leftward as well as rightward saccades. Mean speeds during the 100 ms post-saccadic period varied between 1 and 4 deg/s for most of the saccades. Vergence drifts, calculated as the mean velocity during a 200 ms period starting 120 ms after the saccade offsets, were

still directed in the convergent direction, but the velocities had decreased to below 1 deg/s for all saccade amplitudes. Vergence records reproduced in Fig. 7 show the vergence component of post-saccadic drifts as a continuation of the vergence movement occurring during the horizontal saccade. The binocular fixation errors, which were present at the end of all horizontal saccades, were removed within a

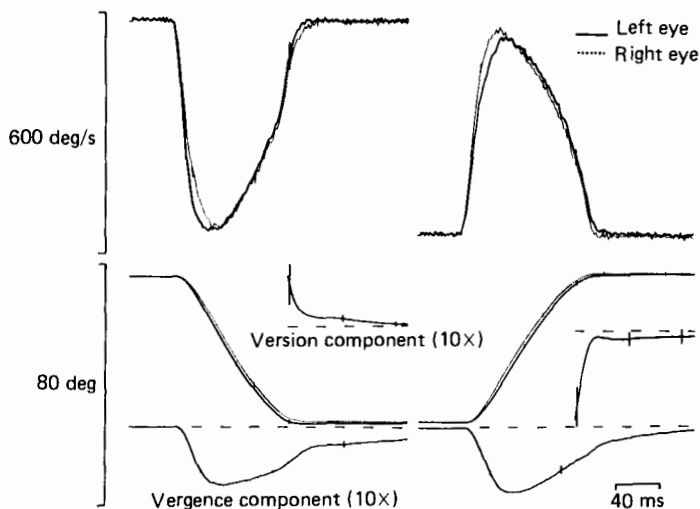


Fig. 7. Velocity (top) and position (bottom) profiles (means of four saccades made by subject C.E. within one trial) of 50 deg saccades made in the leftward (left diagrams) or rightward (right diagrams) direction. The computed vergence and version components have been amplified by a factor 10 for reasons of clarity. Vergence = $L - R$ horizontal eye position; version = $(L + R)$ horizontal eye position/2; version is only shown for last part of saccades. Dashed horizontal lines have been added to show the post-saccadic drift more clearly. Vertical bars in the traces indicate ± 1 s.d.

period of about 300 ms. As will be shown by its persistence in monocular viewing conditions, post-saccadic vergence drift was largely pre-programmed and independent of a visual disparity stimulus. In addition to vergence, post-saccadic drift also showed a conjugate component. These version drifts depended on the direction of the saccadic movements. Binocular pairs of leftward saccades showed version drift to the left; pairs of rightward saccades showed version drift to the right. Version drifts were smaller than vergence drifts. The overall result of the combined, unequal drift in version and vergence was a slow post-saccadic drift (less than 1 deg/s) of the abducting eye opposite to the saccade direction, while the post-saccadic drift of the adducting eye was faster (between 1 and 3 deg/s) and in the same direction as the saccade.

Saccades between central and eccentric targets

In the previous section we showed that temporal saccades were different from nasal saccades. However, the eyes behaved symmetrically with respect to the median plane: leftward saccades of one eye showed the same characteristics as rightward

saccades of the other eye. For eccentrically located saccades, i.e. saccades between the central fixation point and a peripheral target, parameter differences between binocular, paired saccades were similar to those for saccades around the central fixation point. Eccentric saccades, however, showed an additional asymmetry, related to their centrifugal or centripetal direction.

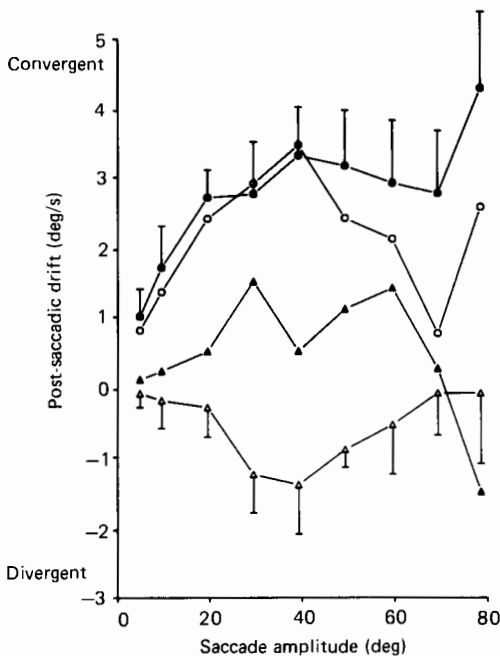


Fig. 8. Vergence (circles) and version (triangles) components of post-saccadic drift (means of three subjects) after leftward (open symbols) or rightward (filled symbols) saccades, calculated over a period of 100 ms, starting 20 ms after saccadic offset. Convergent and conjugated, rightward drift are plotted as positive values. Vergence = $L - R$ horizontal eye position; version = $(L + R)$ horizontal eye position/2. Data were obtained from saccades made symmetrically about the primary position. The vertical bars indicate 1 s.d.

Figure 9 shows the maximum speed, duration and skewness *vs.* amplitude relationships for eccentric saccades.

The maximum speeds of centripetal saccades agreed well with maximum speeds of saccades around the central fixation point (Fig. 4), except for centripetal saccades of 40 deg which attained lower maximum speeds. Centrifugal saccades with amplitudes between 10 and 40 deg were considerably slower. For saccades larger than 20 deg the maximum speeds were between 10 and 20% lower than for centripetal saccades. It was, therefore, to be expected that their durations would also differ because large centripetal and centrifugal saccades differed so much with respect to their maximum speeds.

Indeed, centrifugal saccades larger than 15 deg had significantly longer durations ($P < 0.01$) than corresponding centripetal saccades (Fig. 9). Durations of both

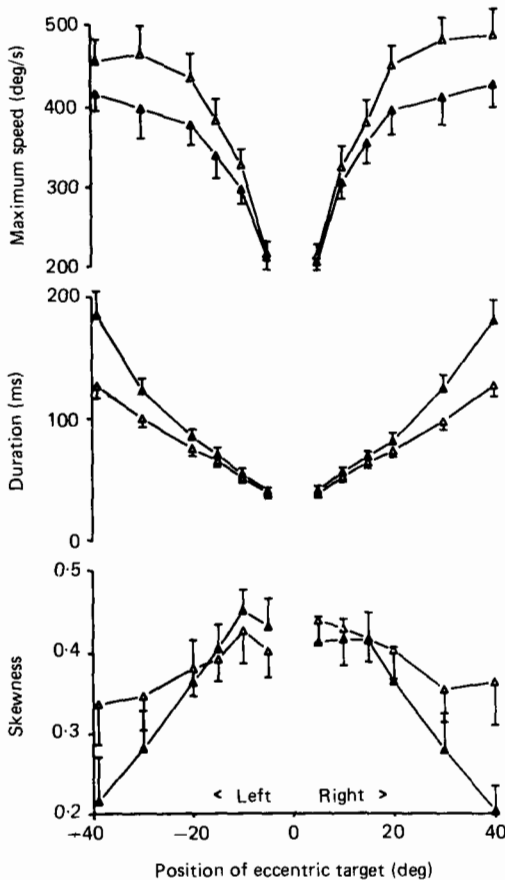


Fig. 9. Maximum speed (top), duration (middle) and skewness (bottom) of eccentric saccades (means of three subjects). Results for centrifugal (filled symbols) and centripetal (open symbols) saccades were obtained from data of the two eyes. The vertical bars indicate 1 s.d.

centripetal and centrifugal saccades were described well by linear functions, with different parameters:

$$\text{Centripetal: duration} = 2.5 \times \text{amplitude} + 27 \text{ ms} \quad (r^2 = 0.99),$$

$$\text{Centrifugal: duration} = 3.9 \times \text{amplitude} + 13 \text{ ms} \quad (r^2 = 0.98).$$

The linear relationship between saccade duration and amplitude for centripetal saccades was very similar to that for saccades around the central fixation point, but it was rather different for centrifugal saccades.

In addition to these differences in maximum speed and duration, centripetal and centrifugal saccades also differed in the shape of their velocity profiles. Centrifugal saccades were much more skewed than centripetal saccades as shown in Fig. 9. The minimum skewness value reached was about 0.20, as was the case for saccades made symmetrically around the primary position.

For large saccades the following order of skewness could be observed: centrifugal saccades were extremely skewed (very low skewness values), saccades around the central fixation point were somewhat less skewed and centripetal saccades were almost symmetrical. The very skewed shape of centrifugal saccades might give the false impression that the period of acceleration was extremely short for such saccades. The asymmetry, however, was completely caused by prolonged deceleration.

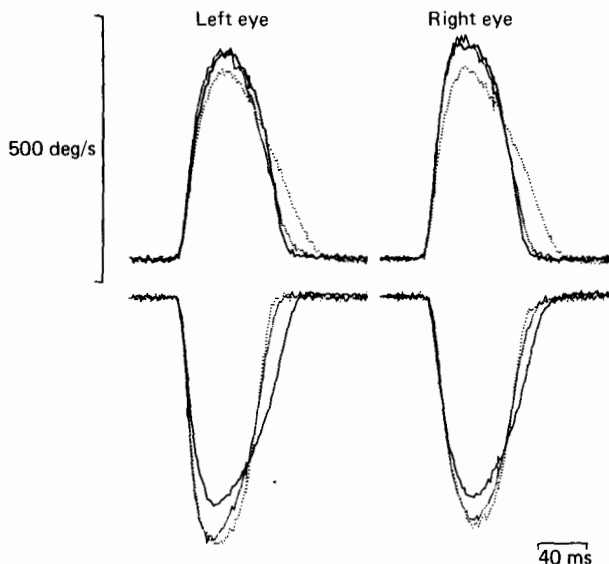


Fig. 10. Velocity profiles (means of four saccades made by subject C. E. within one trial) of rightward (top) and leftward (bottom) saccades of 30 deg. The saccades were made eccentrically in the left oculomotor range (continuous lines), symmetrically about the centre (fine dotted lines) or eccentrically in the right oculomotor range (coarsely dotted lines).

tion phases, as shown in Fig. 10 for 30 deg saccades. Acceleration phases of centripetal and centrifugal saccades were very similar in duration, although maximum speeds of the latter were smaller. These smaller speeds, resulting in smaller covered distances at the moments of maximum speed, were compensated by slower decreases in speed during the periods of deceleration.

The accuracy of centripetal, as well as centrifugal, saccades was similar to that of saccades made symmetrically about the primary position, i.e. mean errors did not exceed about 0.5 deg. The only exception was formed by saccades towards 40 deg eccentric, a position close to the limit of the oculomotor range which some subjects could with difficulty reach or hold and for which saccades were hypometric by 1.5 deg on average. The same mechanical problem probably caused the relatively large hypometria of symmetrical saccades with an amplitude of 80 deg (Fig. 3, lower panel).

Saccadic trajectories in the fronto-parallel plane

The relationship between maximum speed and amplitude of horizontal saccades showed only modest variability of the component along the horizontal meridian. The vertical components of what were, in principle, 'horizontal saccades' were

investigated by inspection of trajectories of eye movements, projected onto the fronto-parallel plane. Examples of such trajectories followed by the two eyes are shown in Fig. 11. The lower vertical level of *B* than of *A* reflects a small deviation of the LED arrangement from the horizontal plane. The maximum vertical difference between *A* and *B*, which was consistent for all the subjects, was 1.5 deg for 80 deg saccades. A conspicuous feature of larger saccades in particular was that their

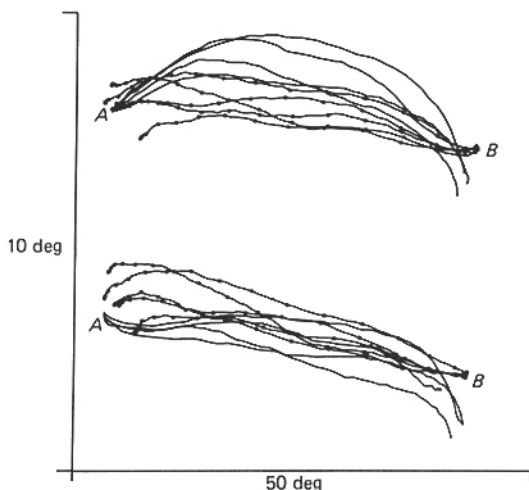


Fig. 11. Trajectories of single, 40 deg saccades in the fronto-parallel plane (subject C. E.). The saccades of the left (top) and right (bottom) eye were made symmetrically about the primary position, except for a slight difference in height (*A* being located slightly higher than *B*, as turned out in the analysis of the data). *A* indicates the starting point of rightward (continuous lines without dots) saccades; *B* indicates the starting point of leftward (continuous lines with dots) saccades.

trajectories were curved. The angle between the initial slope of the saccadic trajectory and the line connecting the start and end positions of the primary saccade varied between 5 deg in the downward and 20 deg in the upward direction. The majority of the saccades started in the upward direction and subsequently deflected downwards to their final position. Trajectories of rightward saccades usually differed from those of leftward saccades of the same eye. Such differences were idiosyncratic for a particular eye and subject. Paired saccades of the two eyes usually followed unequal trajectories too. Figure 11 shows binocular saccades with amplitudes of about 40 deg. The angle between initial slopes of the saccadic trajectories of the two eyes was larger than 20 deg for rightward movements in this example. This shows that the movements of the two eyes were also rather poorly yoked in direction. The degree of yoking was better at the end of primary saccades. Maximum deviations of saccades from the line connecting the horizontal targets were typically smaller than 1 deg for saccades up to 20 deg, but about 4 deg for saccades larger than 60 deg.

Effect of viewing conditions

Experiments in which binocular and monocular viewing were interleaved were done to investigate whether viewing conditions affected saccadic parameters of the

seeing as well as the non-seeing eye. The effects of viewing conditions on the maximum speed, duration and skewness of saccades in relation to their amplitude were not significant ($P > 0.05$). Thus, saccade parameters remained unchanged, irrespective of whether the saccades were made with monocular or binocular visual input. Eye movements during monocular viewing, however, were less well yoked than during binocular viewing. The non-seeing eye tended to drift, in most cases to

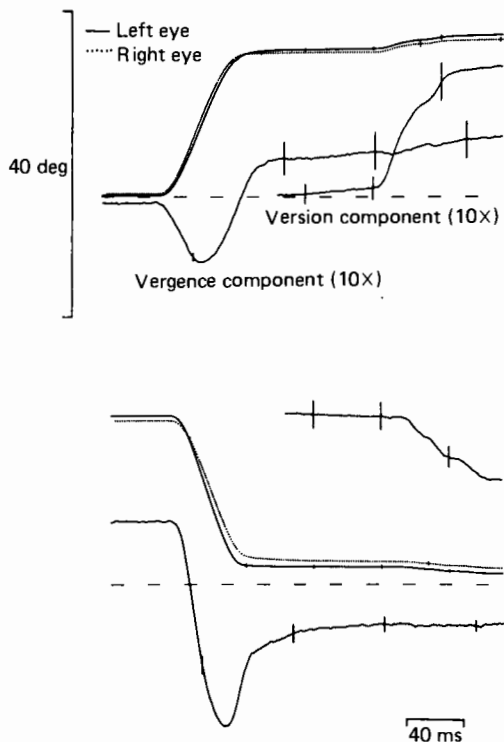


Fig. 12. Position profiles (means of four saccades made by subject C.E. within one trial) of 20 deg saccades made in the rightward (top) or leftward (bottom) direction. Viewing was monocular, with the right eye covered. The computed vergence and version components have been amplified by a factor of 10 for reasons of clarity. The dashed lines indicate the vergence angle in case of perfect binocular fixation of the targets. Vertical bars in the traces indicate ± 1 S.D.

a more central position, during the intervals of fixation between the saccades. As a result, the non-seeing eye was not accurately directed to the target position at the beginning of saccades. This is shown in Fig. 12. The amplitudes of saccades also showed larger differences between the two eyes with monocular than with binocular viewing. Amplitudes of saccades of the non-seeing eye tended to be smaller. Larger amplitudes, however, were also observed. The increased inequality in saccadic amplitude of the two eyes during monocular viewing affected vergence in the following ways. Vergence amplitudes were generally larger (up to about 4 deg). Vergence errors remained present after saccade offsets in the divergent or convergent direction. Post-saccadic drift, however, occurred with monocular viewing

just as it had with binocular viewing. Neither the vergence nor the version component of post-saccadic drift were affected by viewing conditions. As a result of changed vergence amplitudes in combination with unchanged post-saccadic drift, vergence errors remained present after saccades with monocular viewing. These vergence errors were not compensated during the intersaccadic fixation period and, therefore, created offsets for the non-seeing eye at the beginning of the subsequent saccades.

DISCUSSION

Comparison of saccadic parameters with prior research

Our instrumentation allowed us to measure the relationships for maximum speed, duration and skewness *vs.* amplitude of horizontal saccades precisely and accurately over the full oculomotor range. The mean values of maximum speeds observed agree well with many previous reports, which usually covered a smaller range (Boghen *et al.* 1974; Baloh *et al.* 1975; Schmidt *et al.* 1979; Abel, Troost & Dell'Osso, 1983; Fuchs & Binder, 1983), but not with Bahill *et al.* (1975, 1981) who reported maximum speeds about twice as high as those observed in the present experiments. The functional relationship we observed, however, can be described only approximately by simple mathematical relations. Maximum speed *vs.* amplitude relations have been characterized by power law (Schmidt *et al.* 1979), as well as exponential curves (Baloh *et al.* 1975; Bahill *et al.* 1981). It is clear from our results that power-law functions describe the asymptotic behaviour for large amplitudes poorly, but also that exponential fits are not quite appropriate to describe the data over the full saccadic range. Estimation of maximum speeds of large saccades on the basis of exponential fits of small-amplitude data underestimate the true performance of the human saccadic subsystem.

Baloh *et al.* (1975) found that the duration of saccades was linearly related to their amplitudes for saccades from 6 to 90 deg. We find, however, that saccades larger than 50 deg last disproportionately longer (Fig. 5). For these large saccades, the maximum speed and skewness parameters also cannot be extrapolated correctly from similar parameters of smaller saccades. Maximum speed increases and the velocity profile becomes more skewed for increasing amplitudes up to about 50 deg. For larger saccades, maximum speeds remain constant (Fig. 4) and velocity profiles keep the same degree of skewness (Fig. 6). The velocity profiles of such large saccades are very similar during their initial acceleration phases. However, the period in which speed is maintained near its maximum level increases together with the duration of deceleration as a function of the amplitude of the saccade. As a result of the extension of the top of the velocity profile, the time between saccade onset and peak velocity, as well as its variability, increases for larger amplitudes. The skewness remains about the same, because the period of deceleration also increases.

Several authors (Hyde, 1959; Baloh *et al.* 1975) have reported that the skewness of saccadic velocity profiles increases as a function of amplitude. Recently, Van Opstal & Van Gisbergen (1987) found that skewness correlated better with saccade duration than with amplitude. Saccades with longer durations were more skewed. In their experiments, however, only centrifugal saccades were studied. It has even been suggested that the skewness *vs.* duration relation might be an invariant property,

common to all saccades (Smit, Van Gisbergen & Cools, 1987). Our results do not support this view. Skewness and duration of centrifugal and centripetal saccades clearly show that a tight relation between skewness and duration does not exist. For instance, Fig. 9 shows that centrifugal saccades of 30 deg had the same durations as centripetal saccades of 40 deg. Yet, the skewness of these saccades was rather dissimilar. In the more intimately related paired saccades of the two eyes, skewness and duration did not follow the suggested relationship either. The velocity profiles of saccades made by the abducting eye were more skewed than those made by the adducting eye. However, the saccades of the abducting eye had slightly shorter durations than those of the adducting eye. Clearly, the relationship between skewness and duration is not tight.

Accuracy and variability of saccades

We found that the amplitudes of small, as well as large, primary saccades were accurate (Fig. 3). This finding is in contrast with the general belief that primary saccades undershoot their targets by about 10% (Becker & Fuchs, 1969; Becker, 1972; Henson, 1978; Prablanc, Massé & Echallier, 1978; Pelisson & Prablanc, 1988). The accuracy of saccades might be related to the experimental paradigms used. In our experiments the targets were visible at all times in a dimly illuminated, but highly structured, visual environment. These conditions rendered the target positions clearly visible. Subjects were uncertain about the target positions in the experiments of Becker (1972) and Henson (1978), because a saccadic eye movement had to be made to a target position as soon as the target was lighted. Reinterpretation of a finding of Kapoula & Robinson (1986) may also support this suggestion. These authors found that centripetal saccades were more accurate than centrifugal saccades. However, the centrifugal targets were pseudo-randomly selected and, therefore, their probable future position was less well known to the subject than the centripetal target, which was always at the known central fixation position from which all centrifugal saccades were made. Kapoula & Robinson (1986) found a mean undershoot of 0.3 deg for the centripetal saccades, a value which agrees well with our results. Their result, however, is likely to reflect an asymmetry in demands of the task they chose to employ, rather than an asymmetry in the saccadic subsystem itself. As discussed by Zingale & Kowler (1987), in daily life most saccades are made to targets which are stationary or at least present for a prolonged period of time. Our results suggest that saccades are normally accurate within a few tenths of a degree under such natural conditions, although this will have to be confirmed under conditions with the head unrestrained.

Our maximum-speed data were considerably less variable than those which have been reported in the literature. Obvious reasons for such good precision are the accurate and precise eye movement recording method, the selective pooling of data and the experimental paradigm used. We believe that our recording technique with its inherent absolute calibration had particularly beneficial effects on intersubject variability. Our data-pooling method also helped. Comparison of Fig. 4 with Fig. 9 shows that pooling of saccades around the central fixation point with eccentric saccades would have drastically increased our intrasubject variability, obscuring many important features of oculomotor performance. Recently, Smit *et al.* (1987)

showed that variability, as well as values of saccadic parameters, differed in different experimental paradigms: difficult tasks led to more variability. The experimental paradigm used in our experiments was very simple, as well as natural, which may well have contributed to the small variability observed. The voluntary nature of the generation of saccades in our experiment probably also precluded significant fluctuations in alertness, which are a further source of variability. We may add that in our sample no effects related to age (35–60 years) could be observed.

Vergence changes associated with saccades

Until now, very little direct information has been available about the degree of yoking of the eyes during relatively large saccadic eye movements. Our understanding was based mainly on monocular recordings and the observation that abducting saccades of one eye are accompanied by adducting saccades of the other eye. Thus, in most cases, statistical differences between monocular saccades in different directions have been interpreted in terms of yoking of the two eyes. This has produced confounding interpretations (Fuchs, 1971). Abel *et al.* (1979), using electro-oculogram (EOG) recordings of each eye apart, were unable to find a consistent nasotemporal asymmetry. Our findings on differences between maximum speed and duration of nasal and temporal saccades are in agreement with results reported by Robinson (1964). He observed, from monocular recordings of saccades made between monocularly viewed targets, that nasal saccades were slower and lasted longer than temporal saccades, and inferred that this would result in a transient uncrossed disparity of as much as 2.5 deg for 15 deg saccades. The present binocular recordings show that the differences between saccades of the two eyes are very stereotyped. Binocular horizontal saccades are always accompanied by transient divergent binocular fixation errors of up to several degrees which decrease to about 0.3 deg at the offset of each saccade larger than 5 deg.

One possible reason for this transient divergence could be an inhibitory interaction between the saccadic and vergence subsystems causing a transient loss of the vergence command during the saccade. This vergence command is necessary for maintaining the vergence angle of 4 deg required for binocular fixation in our conditions. Kapoula, Hain, Zee & Robinson (1987) suggested that diverging movements during saccades were caused by a temporary disconnection of the tonic vergence signal during saccades. This hypothesis could be, in principle, tested by changing the tonic vergence by prism adaptation (Schor, 1983). However, the hypothesis seems rather implausible in view of the normally existing bias of the vergence subsystem: in the dark, a mean convergence of 3.22 deg (corresponding to a distance of 116 cm) has been reported by Owens & Leibowitz (1980). This suggests that in our stimulus conditions virtually no vergence effort was required.

Mechanical asymmetries in the orbital plant provide another potential explanation. Collins, Carlson, Scott & Jampolsky (1981) shown that the stiffness when the left eye was rotated in the nasal direction was about 11 % greater than the stiffness when the same eye was rotated in the temporal direction.

The occurrence of disjunctive eye movements, associated with saccades between targets located on an iso-vergence surface, appears to constitute a violation of Hering's law. As has been discussed by Howard (1982) and Ono (1983), the

substance of Hering's law and even its falsifiability are somewhat elusive. In its extreme form, Hering's law reduces to the statement that any eye movement can be described as the sum of two components: a conjugated version (with the two eyes moving through equal angles in equal directions) and a disjunctive vergence (with the eyes moving through equal angles, but in opposite directions). This, however, is a meaningless mathematical tautology which could gain intrinsic value only by the demonstration that vergence and version are controlled by independent neural processes, adding linearly at the output level. As steps between targets differing only in direction would be expected to engage solely the version subsystem, the concomitant vergence changes we observed appear to violate at least the spirit of Hering's law.

What are the implications of transient vergence changes for vision? Clearly, transient vergence changes are associated with all horizontal saccades; these will cause transient changes in absolute disparities, i.e. fixation disparities. Fortunately, binocular fixation errors below a certain limit do not interfere with the visual perception of the world. Vergence eye movements induce absolute disparity changes between the two retinal images but leave relative disparities between objects unchanged. It has been shown recently that vergence is neither a cue for depth, nor does it interfere with the perception of motion in depth on the basis of relative disparity (see Steinman *et al.* 1985; Regan, Erkelens & Collewijn, 1986). Therefore, binocular fixation errors after saccades may remain unnoticed by the observer and may have little significance for the processing of visual information.

Centripetal-centrifugal asymmetries

Our results corroborate earlier observations (as cited in the Introduction) that centripetal saccades have faster dynamics than centrifugal saccades. Whereas centripetal saccades reached about the same velocities as those made symmetrically about the primary position, centrifugal saccades were distinctly slower, lasted longer and were more skewed, due to a prolonged deceleration phase. Even the largest centripetal saccades (40 deg) did not attain velocities higher than about 500 deg/s, which seems to be the upper limit of human eye velocity. Our results for 20 deg saccades are in good quantitative agreement with the recent observations by Pelisson & Prablanc (1988). These authors speculated that this asymmetry could be in part due to essential non-linearities in the pulse-step commands to the agonist and antagonist muscles. In the antagonist, the pulse consists of a total deactivation; as negative activities obviously do not exist, the effective contribution by this inhibition to the net change in forces acting on the eyeball is largest when the preceding activity of the antagonist is high, i.e. when the eye starts in an eccentric position. In combination with a saturation of the maximal pulse activity of the agonist, this would be a source of asymmetry. However, mechanical properties of the orbital plant are also likely to contribute to the asymmetry. Collins (1975) found that saccadic peak forces of agonist muscles, measured under isometric conditions, were much higher for centrifugal than for centripetal saccades. The passive orbital elasticity tends to pull the eyeball towards the primary position (see e.g. Robinson, 1981). This force alone should introduce an asymmetry between centrifugal and centripetal movements. In summary, neural as well as mechanical inhomogeneities

are likely to affect the shape of saccades as a function of direction and initial position. Our results suggest that the saccadic subsystem will move the eye accurately to the desired position in the shortest time compatible with the momentary initial conditions. The system does not maintain a uniformly constant shape for all saccades, which it could do only by slowing down all saccades to the level permitted by the worst conditions.

Implications of post-saccadic drift for binocular fixation

Our data showed that the vergence component of post-saccadic drift is a continuation of the vergence movement, occurring during saccades. Post-saccadic vergence drift removed fixation errors caused by unyoked saccades. Our data also showed that the version component of post-saccadic drift was target directed. These observations imply that post-saccadic drift is functional. The fovea of each eye is shifted towards the target by post-saccadic drift. It is obvious that post-saccadic drift has to be unequal in the two eyes, because the vergence and version components enhance each other in one eye but oppose each other in the other eye. The fact that abducting saccades were a few tenths of a degree larger than paired adducting saccades in combination with the usually small undershoot of the primary saccades (Fig. 3) implies that the target was closer to the fovea of the abducting eye than to the fovea of the adducting eye after horizontal saccades. Fortunately, the abducting eye showed the least post-saccadic drift. This means that the better conditions for vision with respect to retinal position of the target, as well as with respect to its retinal slip, were united in one eye. Kapoula *et al.* (1987) showed that after 3 days of monocular vision the post-saccadic drift of the seeing eye after adducting saccades had decreased to the level of drift after abducting saccades. This finding suggests that the visual system does not tolerate large post-saccadic drifts during monocular viewing but cannot avoid these vergence movements during binocular viewing. It is generally assumed that conjugate saccades are generated by one pulse-step signal sent to the motoneurons of the appropriate muscles of the two eyes. This construction makes corrections in a single eye, leaving the other eye untouched, impossible. However, Vilis, Yates & Hore (1985) and Viirre, Cadera & Vilis (1987) showed that after a few days, during which one eye of monkeys was patched, the non-seeing eye usually made smaller saccades than the seeing eye. Our data show that saccade amplitudes become more unequal and less reproducible in the two eyes *immediately* after loss of binocular vision. This means that binocular vision is essential for keeping the amplitudes of binocular saccades as equal as possible, a result which strongly suggests that adaptation of the pulse-step signal is possible for a single eye.

Generation of binocular horizontal saccades

During saccades, ocular motoneurons show a burst-step change in firing rate (Fuchs & Luschei, 1970; Robinson, 1970). The burst is due to the activity of medium-lead burst neurons located in the pontine reticular formation (Van Gisbergen, Robinson & Gielen, 1981). Firing rate as well as duration of motoneuron bursts are related to saccade amplitude. The dependence of both the initial slopes of the velocity profiles (Fig. 2) and the saccadic duration (Fig. 5) on saccade amplitude

supports the idea that the level, as well as the duration, of the total motoneuronal output are adjustable. Our results suggest that all motoneurons are recruited and fire maximally during the bursts they make to generate 50 deg saccades. This would leave the durations of the bursts as the only controllable parameter for the generation of larger saccades. This possibility has been suggested before.

Abel, Schmidt, Dell'Osso & Daroff (1978) patched the paretic and non-paretic eye of one patient alternately and found that saccades made by the viewing eye became orthometric. From the unchanged maximum speeds of saccades, these authors concluded that the change in saccade amplitude was accomplished by changing the duration of the saccadic pulse alone, without a change in its height. Adaptability of the saccadic pulse duration alone may explain why abducting and adducting saccades were so stereotypically different. It may indicate that pulse height is coupled to saccade amplitude, but pulse height is independent of muscle properties. In that case, the mechanical differences of the eyes for abduction and adduction (Collins *et al.* 1981) would not be compensated by the saccadic subsystem. Completely yoked eye movements during the acceleration phase would result automatically in saccades with different amplitudes in the two eyes. Thus, either the initial part of acceleration or the saccadic amplitude can be made equal in the two eyes. Apparently, the saccadic subsystem prefers the latter option.

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