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BINOCULAR CO-ORDINATION OF HUMAN VERTICAL SACCADIC EYE MOVEMENTS

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SUMMARY

1. The binocular co-ordination of human vertical saccades was analysed systematically over the full oculomotor range, with a precise and accurate scleral sensor coil technique. Effects of amplitude (1·25–70 deg), direction (upward *vs*. downward and centripetal *vs*. centrifugal), as well as position (upper or lower sector of vertical oculomotor range), were investigated systematically in three subjects.

2. All saccades were made voluntarily between continuously presented pairs of targets, which subtended equal angles of target vergence.

3. Vertical saccades were less accurate than horizontal saccades (as described by Collewijn, Erkelens & Steinman, 1988). For target distances between 10 and 70 deg, upward saccades undershot the target by about 10%, whereas downward saccades tended to overshoot the target. Downward saccades were about 1·5 deg larger than upward saccades between the same targets.

4. Peak velocities continued to increase monotonically with saccadic amplitude up to 513 ± 27 (S.D.) deg/s for 70 deg saccades; a distinct asymptotic level was not reached.

5. Velocity profiles of upward and downward saccades, made symmetrically about the primary (straight-ahead) position, were very similar for amplitudes up to 30 deg. At larger amplitudes, velocity profiles of upward saccades remained single peaked, whereas those of downward saccades invariably developed a second velocity peak.

6. Parameters of upward saccades depended heavily on the position of the eye. In the upper oculomotor range such saccades had lower maximum speeds, longer durations, and were more skewed than similar saccades in the lower oculomotor range (below primary). Downward saccades were almost independent of eye position.

7 Vertical eye movements during vertical saccades were virtually identical in the two eyes. In contrast, disjunctive horizontal components were systematically present. Upward saccades, at all amplitudes, were associated with diverging eye movements. Converging eye movements occurred during downward saccades. These systematic effects suggest that the vergence subsystem is not turned off during saccades.

8. These changes in vergence were followed by converging horizontal post-saccadic drift after upward saccades, and in diverging horizontal drift after downward saccades. Vertical post-saccadic drift consisted mainly of a conjugated component, directed towards the target position. We conclude that post-saccadic drift on the vertical meridian is effective in decreasing binocular fixation errors in a way similar to error reduction following horizontal saccades.

INTRODUCTION

Vertical saccades, unlike horizontal saccades, have rarely been investigated systematically, mainly because most eye movement recording systems cannot measure them reliably. The vertical electro-oculogram is heavily contaminated by lid movement artifacts (Barry & Melvill-Jones, 1965). Infra-red limbus tracking methods also show serious distortions in the vertical direction (Yee, Schiller, Lim, Baloh, Baloh & Honrubia, 1985). Therefore, earlier descriptions of vertical saccades, relying on infra-red reflection (Täumer, Lemb & Namislo, 1976), may be unreliable. Such problems are absent with the scleral search coil technique (Yee *et al.* 1985), which, at the moment, is the only reliable method for recording vertical saccades binocularly through the entire oculomotor range. Although this technique has found some application in the study of oculomotor pathology (Leigh, Newman & King, 1982), no valid data base, covering a wide range of vertical saccades, is available at present.

In the present study we measured vertical saccades in both eyes, at amplitudes ranging up to 70 deg, thus covering the entire oculomotor range. As in the previous study (Collewijn *et al.* 1988), which was concerned with binocular horizontal saccades, one goal of this study is to assess the accuracy of vertical saccades and to characterize their shape by maximum speed, duration and skewness parameters. A second goal is to study systematic effects of direction and initial position on saccadic profiles.

A further point of major interest is the degree of yoking between the eyes. A first question in this respect is whether vertical saccades of the two eyes are identical in amplitude and shape. In view of the systematic, mainly transient divergence observed during horizontal saccades, despite the absence of a demand for vergence change (Collewijn *et al.* 1988), a second question is whether systematic horizontal vergence movements are associated with vertical saccades.

We shall show that there are systematic differences between upward and downward saccades, and that the shape of vertical saccades is strongly affected by the position in the oculomotor range where they are made. A brief, preliminary communication of the results has appeared (Collewijn, Erkelens & Steinman, 1987).

METHODS

The recording technique, experimental procedure and data analysis have been described in the preceding paper (Collewijn *et al.* 1988). Briefly, the revolving magnetic field–sensor coil technique recorded binocular eye movements very accurately. Targets were permanently lit pairs of light-

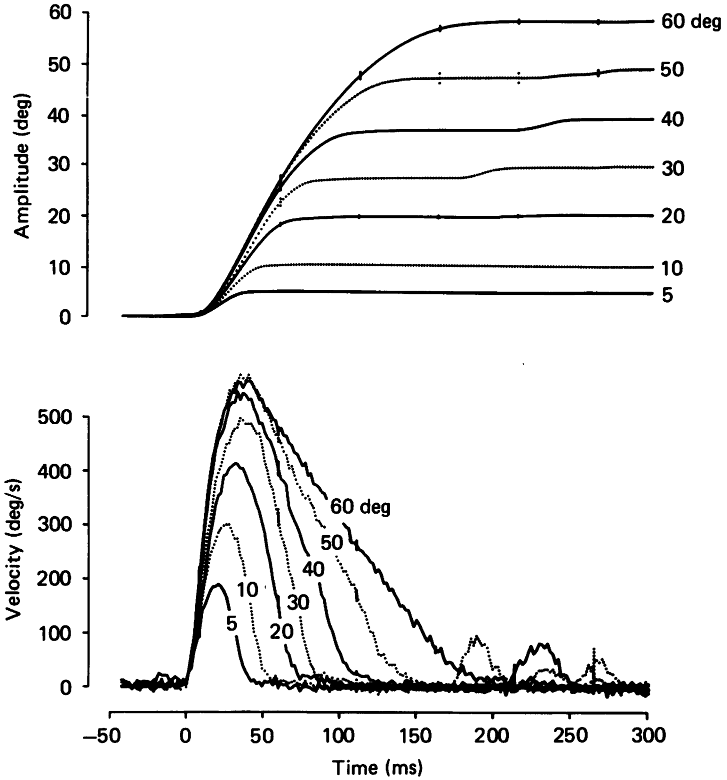

Fig. 1. A family of typical position (top) and velocity (bottom) profiles of upward saccades ranging from 5 to 60 deg, with the beginning and end positions distributed symmetrically around the central position. Each curve represents the average of four saccades of subject C.E. made within one trial; vertical bars indicate ± 1 S.D.

emitting diodes (LEDs), positioned on a vertical iso-vergence circle. The same four subjects served in the experiments; as before they made voluntary saccades between the continuously visible stationary targets viewed in a dimly illuminated room.

RESULTS

Vertical saccades between targets symmetric about the straight-ahead position

Characteristics of binocular saccades

Upward and downward saccades were different in shape. Representative families of position and velocity profiles of upward saccades with amplitudes between 5 and 60 deg are shown in Fig. 1. Small standard deviations in the position, as well as velocity, profiles indicate a high degree of reproducibility for such saccades made between stationary targets. The velocity profiles show that acceleration as well as peak velocity increased with amplitude up to about 40 deg. For larger amplitudes acceleration did not change any more, but peak velocity still increased. The peaks of the velocity profiles were well defined. Acceleration phases were about as long as deceleration phases for small saccades; deceleration phases were progressively prolonged for larger sacades. This resulted in almost triangular velocity profiles. Relatively small corrective saccades, as made by the subject shown in Fig. 1 after 30 and 40 deg saccades, were also very reproducible.

Position and velocity profiles for downward saccades with amplitudes between 5 and 60 deg are shown in Fig. 2. The velocity profiles of downward saccades were less

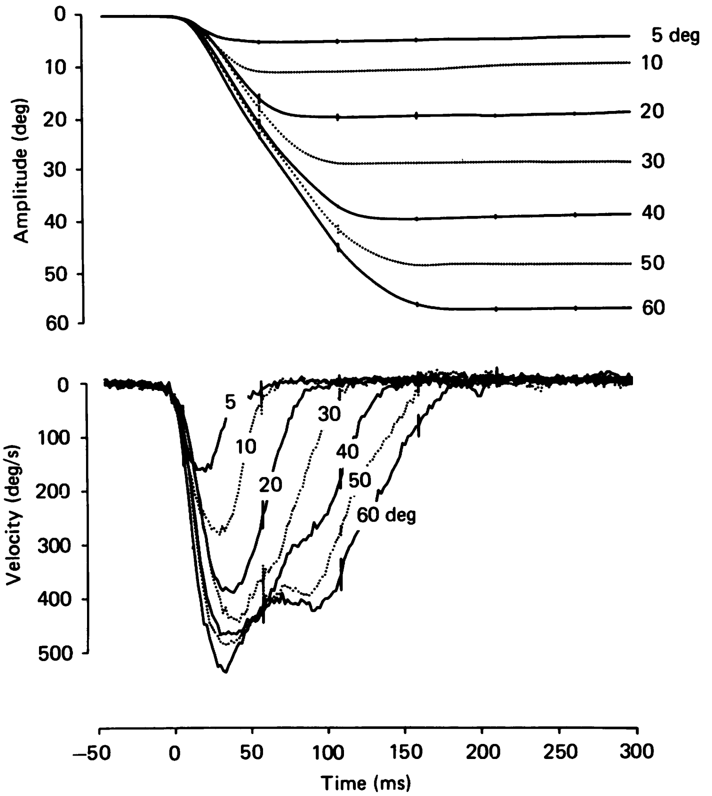

Fig. 2. A family of typical position (top) and velocity (bottom) profiles of downward saccades ranging from 5 to 60 deg, with the beginning and end positions distributed symmetrically around the central position. Each curve represents the average of four saccades of subject C.E. made within one trial; vertical bars indicate ± 1 S.D.

reproducible than those of upward saccades, especially for large amplitudes. The peaks of velocity profiles were less well defined and also the relationship between acceleration and saccade amplitude was not so clear. The velocity profiles tended to develop a second maximum during the deceleration phase for saccades larger than about 30 deg. This second maximum, which became more pronounced for larger amplitudes, was observed in all subjects. The amplitude of the second velocity peak, relative to the amplitude of the first peak, differed among the subjects. Second peaks were even higher than first peaks for subject H.C., the fourth subject, whose data were not used for parameter estimation, for reasons described in the preceding paper (Collewijn *et al.* 1988).

Vertical saccades were less accurate than horizontal saccades. Accuracy differed systematically between the upward and downward directions. In general, primary downward saccades were larger than the corresponding upward saccades made between identical target pairs (Fig. 3). Mean amplitudes of three subjects showed that downward saccades were about 1·5 deg larger than upward saccades between the same targets. In all subjects, downward saccades tended to overshoot the target for target distances up to 40 deg; there was a slight undershoot for larger amplitudes. Upward saccades showed an undershoot, which increased progressively with target distance. This undershoot ranged from 0·8 deg for 10 deg saccades up to 6·7 deg for a target distance of 70 deg.

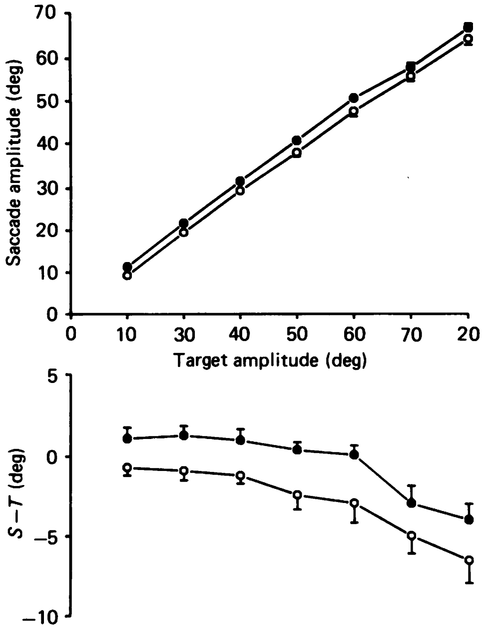

Fig. 3. Amplitudes of saccades (means of three subjects) made between targets located symmetrically about the central fixation point (top). Data from the two eyes have been pooled. ○, upward saccades; ●, downward saccades. Standard deviations were smaller than symbol size at most of the amplitudes. The bottom figure shows the same data but now computed as the difference between saccade amplitude (*S*) and the target amplitude (*T*); *S*−*T* has been plotted against the target amplitude. Vertical bars indicate 1 S.D.

The vertical yoking of vertical saccades was quite good. The group difference between amplitudes of saccades made by the left and right eye was not statistically significant. Two subjects (R.S. and R.D.), however, made slightly, but consistently, larger saccades with the right eye when target distance was greater than 40 deg. The yoking of the eyes with respect to saccade amplitude was almost perfect in subject C.E.

Figure 4 presents the maximum speed, duration and skewness *vs.* amplitude relationships for upward, as well as downward, saccades. The relationship between maximum speed and saccade amplitude was more curved for downward than for upward saccades, but in contrast to our findings for horizontal saccades (Collewijn *et al.* 1988), the maximum speed did not saturate for saccades larger than 40 deg. The maximum speed increased with amplitude up to 513 ± 27 deg/s for upward saccades and up to 487 ± 41 deg/s for downward saccades. There was no significant difference between maximum speeds of upward and downward saccades for amplitudes less than 40 deg, but maximum speeds of upward saccades were higher for larger amplitudes. The effect of eyes was not significant ($P > 0{\cdot}05$). The effect of subjects was significant for downward saccades ($P < 0{\cdot}01$), but not for upward saccades ($P > 0{\cdot}05$). Because the maximum speed did not approach a well-defined asymptotic level at large amplitudes, the data could not be appropriately fitted with an exponential function, the function used to describe the maximum speed *vs.* amplitude relationship for horizontal saccades (Collewijn *et al.* 1988).

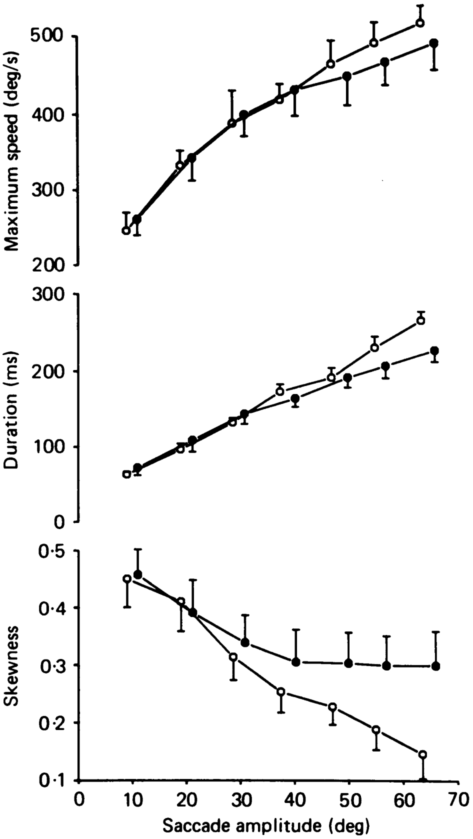

Fig. 4. Maximum speed (top), duration (middle) and skewness (bottom) of saccades made symmetrically about the central fixation point (means of three subjects). Results for upward (○) and downward (●) saccades were obtained from data of the two eyes. Vertical bars indicate 1 s.d.

The relation between saccadic duration and amplitude of vertical saccades was also less straightforward than for horizontal saccades. For saccades up to 30 deg the relationship between saccade duration and amplitude (Fig. 4) was well described by the following linear relation:

$$\text{duration} = 3{\cdot}3 \times \text{amplitude} + 31 \text{ ms} \quad (r^2 = 0{\cdot}99).$$

For saccades larger than 30 deg, the duration increased progressively more steeply as a function of amplitude for upward saccades, whereas it showed soft saturation for downward saccades. Thus, for large amplitudes we found that both maximum speed and duration of downward saccades were smaller than those of upward saccades. This apparent contradiction resulted from the fact that the velocity profiles were so different in shape for large upward and downward saccades (Figs 1 and 2).

Differences between these velocity profiles were also expressed in the relationship between skewness and amplitude (Fig. 4). Velocity profiles of all vertical saccades up to 20 deg were rather symmetrically shaped. Larger upward saccades became progressively more skewed. Skewness values as low as 0·14 were computed for upward saccades of 65 deg. This means that the deceleration phase of such saccades was about 6 times longer than the acceleration phase. Downward saccades showed a different relationship. For saccades larger than 30 deg the profiles became somewhat more skewed. Skewness reached a level of 0·3 where it stabilized. This means that the phase of deceleration was about twice as long as the acceleration phase. Actually, the meaning of the skewness parameter for large downward saccades is questionable, because these saccades showed two local maxima in their velocity profiles.

Disjunctive components of vertical saccades

The yoking of the eyes during vertical saccades was investigated by computing the vertical, as well as the horizontal, disjunctive movements. Disjunctive movements would be absent in case of perfect yoking, because vergence changes were not required by the target configuration. Examples of representative vergence movements associated with 20 deg upward or downward saccades are shown in Fig. 5. Vertical vergence movements were generally small for vertical saccades in either direction. For larger amplitudes, there was a sustained vergence change up to a maximum of about 1 deg in two subjects (R.S. and R.D.), while vertical vergence changes were virtually absent in the third subject (C.E.).

In contrast to this virtually perfect vertical yoking, vertical saccades were accompanied by very stereotyped changes in horizontal vergence. The eyes diverged transiently during upward saccades. The amplitude of this vergence shift varied between 0·5 and 2 deg, depending on the subject and the amplitude of the saccade. The maximum excursion of the diverging movements occurred a little after half of the saccadic duration had elapsed. At saccade offset there was still a net relative divergence varying between 0·2 and 1 deg. Such transient divergence was characteristic of all upward saccades, at all amplitudes and in all subjects. Downward saccades were accompanied by transient convergence. The maximum shift in convergence varied between about 1 and 4 deg, depending on the subject and the saccade amplitude. In comparison with the maximum divergence during upward saccades, the maximum convergence was reached much later during the downward saccades. Therefore, the residual convergence at the end of downward saccades, varying between 0·5 and 2 deg, was larger than the residual divergence at the end of upward saccades. The transient convergence during downward saccades was as stereotyped as transient divergence during upward saccades. It was observed at all saccade amplitudes and in all subjects, including subject H.C.

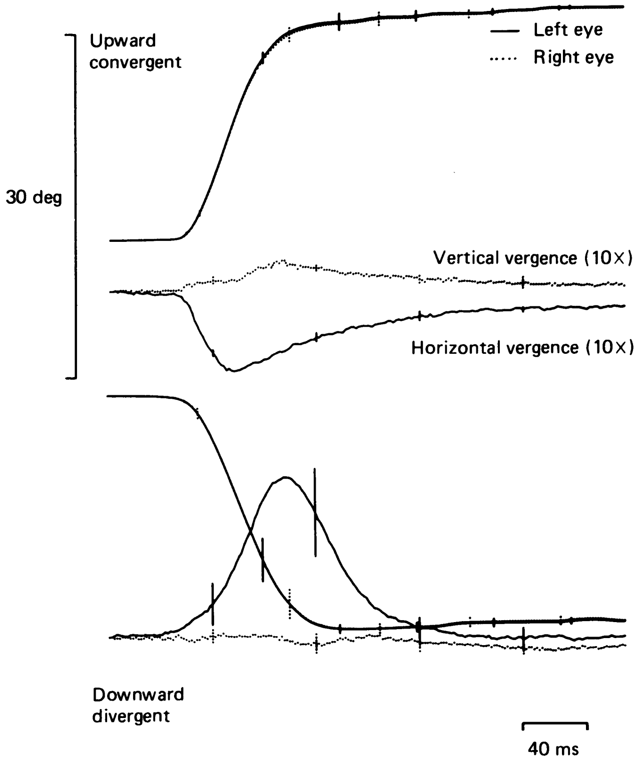

Fig. 5. Typical position profiles (means of four saccades made by subject C. E. within one trial) of 20 deg saccades made in the upward (top) or downward (bottom) direction. The computed vergence components have been amplified by a factor 10 for reasons of clarity. Vertical vergence = $L-R$ vertical eye position; horizontal vergence = $L-R$ horizontal eye position. Vertical bars in the traces indicate ± 1 S.D.

Post-saccadic drift

Post-saccadic drift along the vertical meridian was separated into a version and a vergence component. These components, calculated as the mean velocity during a period of 100 ms, starting 20 ms after saccade offset, are shown in Fig. 6.

Versional drift was upwards after upward, as well as after downward, saccades. After upward saccades mean versional speeds were low, below 1 deg/s, for small amplitudes. Mean versional speed increased with saccade amplitude up to about 3 deg/s. After downward saccades mean versional speeds were rather high, between 1·5 and 3 deg/s, for small saccades. However, in this case the mean speed decreased with saccade amplitude down to 0·2 deg/s for 70 deg saccades. In view of the overshoot observed for downward saccades and the undershoot observed for upward saccades, the results in Fig. 6 show that versional drifts were directed towards the position of the target. Vergence drifts in the vertical direction were negligible after upward, as well as after downward, saccades with amplitudes below 50 deg. There was more vertical vergence drift after larger saccades, although mean vergence speeds were still lower than 1 deg/s.

Mean speeds of horizontal vergence drift are shown in Fig. 7. Horizontal vergence drift depended on the direction in which vertical saccades were made. Convergent drift occurred after upward saccades while divergent drift was observed after downward saccades. Mean speeds of divergent drift were about three times higher than speeds of convergent drift. Inspection of the horizontal vergence traces shown in Fig. 5 reveals that differences between convergent and divergent drift were to be expected. Divergent drifts were continuations of the large converging movements during downward saccades and convergent drifts were continuations of smaller diverging movements during upward saccades.

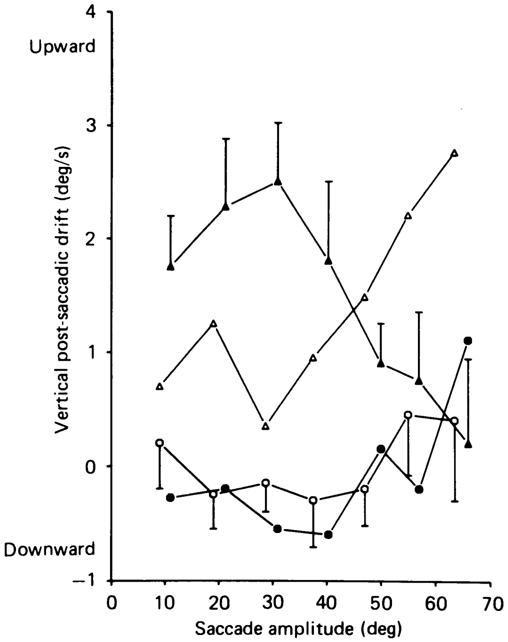

Fig. 6. Vergence (circles) and version (triangles) components of vertical post-saccadic drift (means of three subjects) after upward (open symbols) or downward (filled symbols) saccades. Vertical version = $(L+R$ vertical eye position$)/2$; vertical vergence = $L-R$ vertical eye position. Data were obtained from saccades made symmetrically about the central fixation point. Vertical bars indicate 1 s.d.

Vertical saccades between central and eccentric targets

Differences observed between the velocity profiles, and consequently also between the saccadic parameters, of upward and downward saccades were even more prominent for eccentric saccades. A typical set of 10, 20 and 30 deg upward and downward saccades made in different parts of the oculomotor range is shown in Fig.

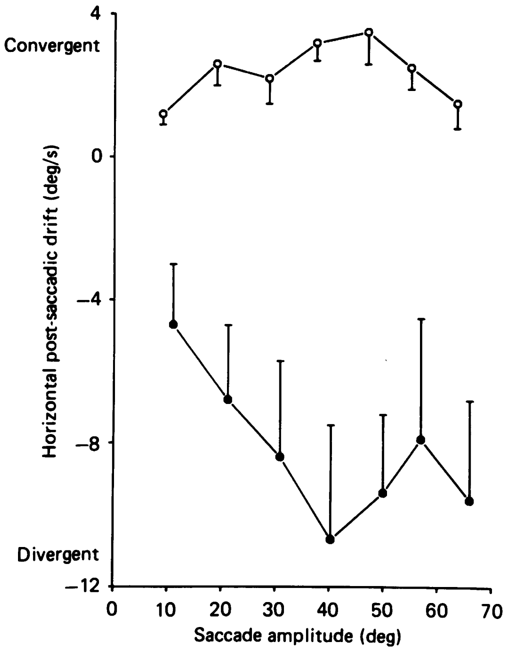

Fig. 7. Vergence components of horizontal post-saccadic drift (means of three subjects) after upward (open symbols) or downward (filled symbols) saccades. Horizontal vergence = $L-R$ horizontal eye position. Data were obtained from saccades made symmetrically about the central fixation point. Vertical bars indicate 1 S.D.

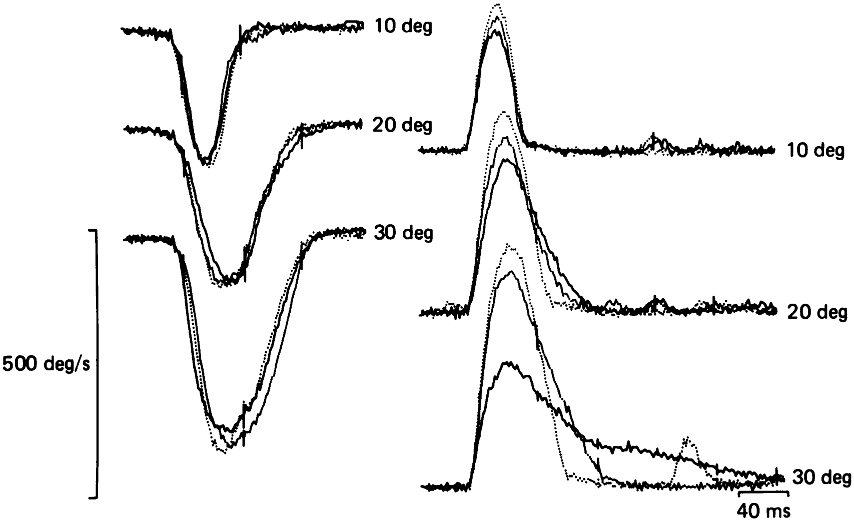

Fig. 8. Velocity profiles (means of four saccades made by subject C.E. within one trial) of downward (left) and upward (right) saccades of 10, 20 and 30 deg. The saccades were made eccentrically in the upper oculomotor range (continuous lines), symmetrically about the centre (fine dotted lines) or eccentrically in the lower range (coarsely dotted lines).

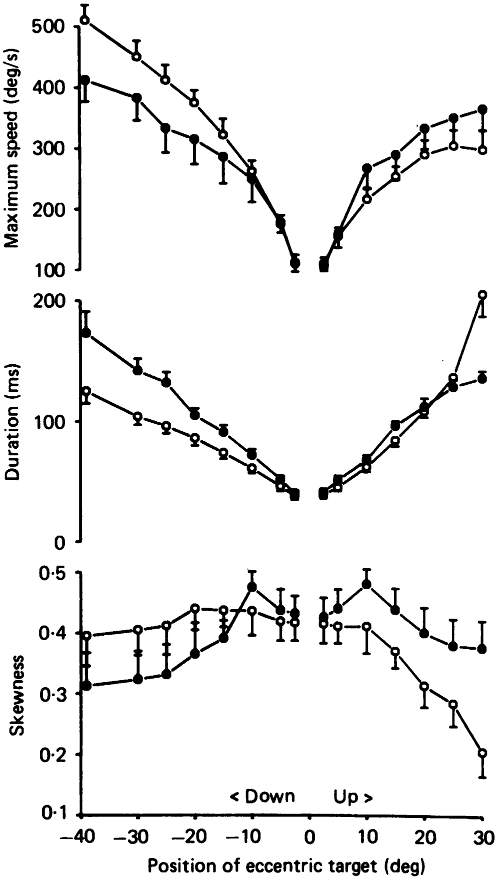

Fig. 9. Maximum speed (top), duration (middle) and skewness (bottom) of eccentric saccades (means of three subjects). Results for upward (○) and downward (●) saccades were obtained from data of the two eyes. Vertical bars indicate 1 S.D.

8. The saccades were made in the upper oculomotor range, symmetric about the central fixation point, and in the lower range, respectively. For downward saccades, the differences between the velocity profiles were very moderate.For 30 deg saccades the maximum speed was slightly higher in the lower oculomotor range, but otherwise the velocity profiles were rather similar. Velocity profiles of upward saccades depended heavily on the part of the oculomotor range in which these saccades were made. The differences between velocity profiles were extreme for 30 deg saccades. These velocity profiles were almost symmetrically shaped, with high maximum speeds of about 450 deg/s in the lower oculomotor range. In contrast, the velocity profiles for similarly sized saccades, made in the upper part of the vertical oculomotor range, showed very low maximum speeds (about 250 deg/s), and the shape of these velocity profiles was very skewed.

The main parameters, i.e. mean speed, duration and skewness of saccades made in the upper or in the lower oculomotor range, are shown in Fig. 9. These parameters describe more precisely the trends shown in Fig. 8. The saccadic parameters were very similar for downward saccades in either part of the oculomotor range, but they were very different for upward saccades. Upward saccades in the upper part of the oculomotor range were by far the slowest saccades made by the subjects, while upward saccades in the lower part of the range were among the fastest. For large amplitudes, upward saccades were even faster than horizontal saccades (Collewijn *et al.* 1988). The low maximum speeds of upward saccades in the upper part of the oculomotor range in combination with their very skewed profiles gave the impression that the eyes had to overcome considerable forces, not present elsewhere in the orbit. A similar impression was gained by the subjects, who mentioned that making large upward saccades in the upper part of the oculomotor range was rather hard.

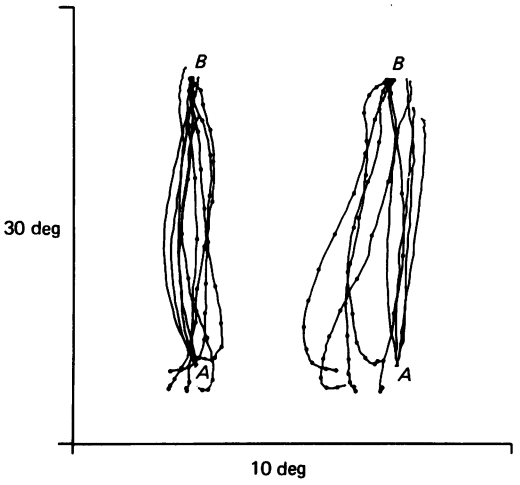

Fig. 10. Trajectories of single, 20 deg vertical saccades in the fronto-parallel plane (subject C.E.). The saccade pairs of the left eye (left side) and right eye (right side) were made symmetrically about the centre. *A* indicates the starting point of upward saccades (continuous lines without dots); *B* indicates the starting point of downward saccades (continuous lines with dots).

Saccadic trajectories in the fronto-parallel plane

The yoking of the eyes during vertical saccades was further investigated by inspection of the saccadic trajectories as projected onto the fronto-parallel plane. Typical examples of trajectories of 20 deg vertical saccades made by the two eyes are shown in Fig. 10. Trajectories of downward saccades were different from those of upward saccades. Downward saccades were generally more curved than upward saccades. Downward saccades showed horizontal components in the nasal direction, in agreement with the convergence shown in Fig. 5. Upward saccades were slightly deflected in the temporal direction, indicating the typical transient divergence. The amount of horizontal deflection was in most cases unequal in the two eyes. Such differences, however, were idiosyncratic. The different horizontal deflections and, therefore, the different movement directions of the two eyes indicated that these were poorly yoked during vertical saccades.

DISCUSSION

Differences between vertical and horizontal saccades

We studied the properties of vertical saccades made by both eyes between stationary targets with distances ranging from 5 to 70 deg. Our main goal was to characterize vertical saccades by maximum speed, duration and skewness parameters. We found that upward saccades were as precise as, but less accurate than, horizontal saccades. Upward saccades tended to undershoot the target. Downward saccades were less precise than horizontal saccades, particularly for large amplitudes. In contrast to upward, as well as to horizontal, saccades, downward saccades generally overshot the position of the target.

Maximum speeds of vertical saccades up to 40 deg were lower than those of horizontal saccades of similar amplitudes. The maximum speeds of vertical saccades showed only the beginnings of saturation for larger amplitudes, in contrast with horizontal saccades where the saturation was more pronounced (Collewijn *et al.* 1988). In other words, the maximum speeds of vertical saccades were higher than those of horizontal saccades for amplitudes larger than 50 deg despite the fact that the reverse was true for smaller saccades.

The main parameters, used to characterize saccades, showed considerable differences between vertical and horizontal saccades. In addition, the degree of accuracy was also rather different. Together these results suggest that vertical and horizontal saccades may be generated by separate subsystems with different properties.

Differences between upward and downward saccades

Except for small, systematic differences in amplitude, upward and downward saccades up to 30 deg were very similar in maximum speed, duration and skewness parameters (Fig. 4), as well as in velocity profiles (Figs 1 and 2). Double-peaked velocity profiles were characteristic for downward saccades with amplitudes larger than 40 deg. At this point we can only speculate on the origin of the second velocity peak. It seems most unlikely that this peak is an artifact caused by the presence of the scleral coils on the eyes because large upward saccades did not show such peaks. The same argument holds against any direct relation between the second velocity peak and eyelid movements during vertical saccades. More probably, large downward saccades are composed of two saccades, the second of which is initiated during the first saccade. Why such double saccades should only occur in the downward direction remains unclear. Closely spaced horizontal saccades have been found previously under certain conditions (Bahill, Bahill, Clark & Stark, 1975).

Dependence of the saccadic parameters on eccentricity

For upward saccades, the saccadic parameters depended heavily on the part of the oculomotor range in which the saccades were made. In particular, upward saccades in the upper range had long durations and low maximum speeds. They were also very skewed. We have inferred from differences between abducting and adducting saccades that the saccadic subsystem programs a specific level for the burst of motoneuronal activity, depending on the desired saccadic amplitude (Collewijn *et al.*

1988). If this is the case, mechanical differences, related to different muscle properties, can only be met by changing the duration of the burst. Evidence for this strategy can be derived from differences observed between upward saccades in different parts of the oculomotor range, as was done foı abducting and adducting horizontal saccades. For example, 10 deg upward saccades in the upper part of the oculomotor range have lower maximum speeds and longer durations than 10 deg upward saccades in the lower part of the oculomotor range (Fig. 8).The higher accelerations (Fig. 8) and higher maximum speeds (Fig. 9) found for 20 deg, compared to 10 deg upward saccades in the upper part of the range, make it clear that the motoneuronal burst has not reached its highest level for the 10 deg upward saccades. Therefore, in principle, 10 deg upward saccades could be executed faster than we observed. Yet, despite the fact that such saccades had to be made repeatedly in our experiments, they never came to be executed faster. Their parameters remained unchanged. Apparently, the saccadic subsystem does not account for mechanical differences due to eccentricity of the eye in the orbit. It prefers to keep the pulse of motoneuronal activity on a level related only to the amplitude of the required saccade. Our results on the vertical meridian thus corroborate a similar conclusion drawn previously from our observations of horizontal saccades (Collewijn *et al.* 1988).

The dependence of the saccadic parameters on eccentricity has been presented in terms of differences between upward and downward saccades (Fig. 9). However, the results can also be interpreted in terms of differences between centrifugal and centripetal saccades, analogous to the analysis that was carried out for horizontal saccades (Collewijn *et al.* 1988). Along the horizontal, as well as along the vertical, meridian, centripetal saccades had higher maximum speeds and shorter durations than centrifugal saccades of equal amplitude. For vertical saccades there was an additional difference between both centrifugal and centripetal saccades made in the upper and lower oculomotor range, a difference which did not exist between horizontal saccades made in the left and right oculomotor range. The differences between saccades made in the upper and lower oculomotor range may indicate that the anatomical resting position of the eyes does not coincide with the visual straight-ahead position, but is located further downward. In this case, the saccades made in the upper oculomotor range were, from an anatomical point of view, actually more eccentric than those made in the lower range. This asymmetry of eccentricity would explain the fact that saccades in the upper oculomotor range had lower maximum speeds and longer durations than those in the lower range of equal amplitude. Eccentricity is a powerful variable.

Vergence changes during vertical saccades

Vertical saccades were accompanied by very distinct vergence movements. The vertical vergence changes were small and idiosyncratic. The horizontal vergence changes, however, were substantial and similar in all of the subjects. Transient divergence was associated with all horizontal, as well as all upward, saccades. However, during downward saccades, the eyes deflected initially in the convergent direction. In view of these findings, explanations suggesting that vergence changes during horizontal saccades are caused by a transient, total or partial loss of the vergence signal (suggested by Kapoula, Hain, Zee & Robinson, 1987, and considered possible by Collewijn *et al.* 1988) can now clearly be seen to be implausible. If the vergence signal would have been lost temporarily, divergence would also have occurred during downward saccades because the vergence angle during the intersaccadic fixation interval was the same for vertical and horizontal saccades. It is not clear why vergence changes occur under conditions where purely conjugated saccades would seem most desirable, It is, however, striking that the vergence changes during vertical saccades correspond to vergence changes actually demanded by most targets in normal, daily vision. For instance, in the case of walking or sitting at a desk, most saccades are made in the lower part of the oculomotor range. Higher targets are usually further away than lower targets. Thus, upward saccades often demand a horizontal divergent component, while downward saccades are often associated with a need for convergence. Although this may seem a gratuitous, teleological argument, it is probably a testable hypothesis. As has become clear in recent years, most of the oculomotor parameters respond adaptively to the particular behavioural requirements to which a subject is exposed. If the systematic vergence changes associated with vertical, as well as with horizontal, saccades reflect adaptation to the most frequently occurring target configurations, they should be specific to well-developed binocular vision. In this case the concomitant changes in vergence we observed should be absent in subjects without functional binocular vision.

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