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Human Eye Movements Associated with Blinks and Prolonged Eyelid Closure

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SUMMARY AND CONCLUSIONS

1. Eye movements associated with eyelid closure were recorded in human subjects with search coils, embedded in self-adhering scleral annuli, in a magnetic field.

2. In contrast to classical notions, voluntary as well as reflex blinks were consistently accompanied by transient downward and nasalward movements of both eyes with amplitudes 1–5°. These eye movements had a shorter duration than the upper lid movements, and the shapes of the spatial trajectories of eye and lid movements were not similar.

3. The trajectory of the eye movements was only modestly affected by gaze eccentricities up to 15°; there was a tendency for the downward component to be enhanced by looking upward, and vice versa.

4. Restraining of the lids of one eye in the open or closed position did not significantly alter the eye movements during (attempted) blinks. Velocity-amplitude-duration relations of the down- and upward components were similar for the same eye before and after closure and for the closed eye and the contralateral unrestrained eye.

5. The velocity-amplitude-duration characteristics of saccades were also unaffected by prolonged closure of the lids of one eye.

6. Prolonged, voluntary closure of the lids was followed by a slow, tonic ocular deviation, which was consistently upward in half of the subjects and consistently downward in the other half. Additional horizontal components were highly variable even within subjects. In one subject the downward deviation was converted into upward deviation when lid closure was mechanically impeded.

7. We conclude that elevation of the eye ball (Bell's phenomenon) does not occur during short blinks and only in about half of the subjects during voluntary unrestrained prolonged lid closure.

8. Our evidence does not support the possibility that the transient eye movements during blinks are caused primarily by a mechanical interaction between the lids and the eye (or the scleral annulus). More likely, they are a secondary effect of an active cocontraction of extraocular muscles that primarily results in retraction of the eye.

INTRODUCTION

The motions of the eye associated with eyelid closure are obviously hard to record by direct observation and by most conventional eye movement monitors. Accordingly, many conflicting results have been reported since Bell (3) published his classical finding of an upward motion of the eye during closure of the lids. Bell's conclusions rested on two key observations (see also Ref. 22). First, he noticed that, in patients with a paralysis of the facial nerve or mechanical impediments preventing normal lid closure, attempted closure was accompanied by elevation of the uncovered eye. This phenomenon has been confirmed many times; however, it is prudent to realize that the movement is associated with a strong and probably prolonged effort to close the defective lids. Bell's second observation concerned ocular motion during a rapid blink. After closing one eye, putting his finger over the closed lid and blinking the other eye, he felt the cornea under the lid roll upward, even "during the most rapid winking motions of the eye lids."

From this rather crude observation emerged the classical notion of Bell's phenomenon occurring generally during every kind of eye closure.

A century passed before serious attempts were made to record the eye movements during blinking. Miles (14, 15), by using a photographic technique, estimated that the eye was elevated 10–15° during each blink. Later investigators using photographic (16), optical lever (8), or unspecified (12) techniques concluded that there were much smaller eye movements during blinks (0° to about 1.5°, usually in the upward and nasal direction). Also, some direct observations of the affected eye in cases of facial paralysis showed only very slight (10) or no visible motion (13) during ordinary blinks of the normal eye. Recent observations using high-speed photography (6) failed to show evidence of Bell's phenomenon in normal fast blinks, but, on the other hand, a considerable posterior movement of the globe (0.7–1.6 mm) occurred consistently. This retraction was recently confirmed (7). Volkmann et al. (21), using a double Purkinje image eye tracker as well as subjective observation of the apparent displacement of a spot moving through a straight trajectory, estimated that just before a normal blink the eyes move downward and inward through about 0.3°.

Apparent but spurious support for the general occurrence of Bell's phenomenon has been inferred from electrooculographic (EOG) recordings. When the lid moves down, vertical EOG traces show a deflection equivalent to an eye elevation of more than 20° (11) or even more than 60° (20). However, it has been demonstrated that such deflections are caused not by vertical ocular rotation, but by the movement of the eyelid over the globe (2, 13). The eyelid acts as a sliding electrode, increasingly shunting the positive corneal pole to the upper EOG electrode while moving downward.

Obviously none of the studies cited has provided unambiguous and complete recordings of human eye movements during blinking, since the methods were unreliable or allowed sampling only in the initial phase of the blink. The electromagnetic search-coil technique (18) seems eminently suited to obtain veridical recordings of the angular eye position, regardless of lid motions. A recent comparison of the EOG and implanted search-coil techniques (19) has shown that the upward EOG deflections during blinking in the monkey are absent in the simultaneous search-coil recordings. Data with implanted coils have been obtained also in the rabbit and guinea pig (7). For humans, some electromagnetically obtained data on blinking have been published by Allik et al. (1), who used a modified technique in which a metal ring without an electrical lead is attached to the eye. These authors reported upward eye movements of 4–9° during blinks.

In view of the confusing state of knowledge on human eye movements associated with eye closure, it seemed appropriate to reinvestigate such movements by using scleral search coils embedded in a self-adhering silicon annulus (5). Our data show conclusively that ordinary blinks are associated with a small downward and inward eye movement, whereas in prolonged voluntary eye closure a tonic deviation follows in either the upward or downward direction.

METHODS

Horizontal and vertical positions of one or both of the eyes were recorded with scleral induction coils embedded in a silicon annulus as described by Collewijn et al. (5) and the electromagnetic induction technique developed by Robinson (18). A properly mounted annulus adheres firmly to the limbus and cannot be shifted across the eye even by manipulation, unless it is first dislodged. To remove an annulus, it has to be grasped with a forceps and lifted from the eye. Blinking and prolonged eye closure are not hampered by the annulus, nor do they interfere with the long-term stability of the coil. Of course, the eyelid movements as such do not affect the signals induced in the coil by the surrounding magnetic field. Actually, frequent blinking is beneficial in experiments using the coil because it keeps the cornea moistened and thereby prevents blurring of vision. The coils were usually inserted with the origin of the lead wire in the nasal canthus. Placement with the lead in the temporal canthus was slightly less comfortable but did not change the shape of the recorded blink-related eye movements. Jiggling of the tightly twisted lead wires did not induce any artifact.

After low-pass filtering at 250 Hz the eye position signals were sampled at a rate of 500/s, digitized with 12-bit precision, and stored on disk by a DEC PDP11/10 computer. The overall resolution and noise was about 1 min of arc with a recording range of 40° (20° in all directions from center). For comparison, the horizontal and vertical DC EOG was recorded simultaneously with the coil signal in a number of cases, by means of conventional EOG electrodes attached with collodion to the skin near the canthi and above and below the eye.

To monitor blinks we also recorded the electroblepharogram (21) from electrodes mounted on the upper eyelid and below the eye. This signal reliably signals the occurrence of blinks, but its shape is hard to interpret, since at sufficient bandwidth (we used 0.1–250 Hz) it contains myographic as well as EOG components.

For a more faithful recording of the lid movements, we used a method very similar to that of Evinger et al. (7). A sagittally oriented light wooden lever (length 12 cm, weight 0.38 g) was balanced on and attached to a transverse taut silk wire as a fulcrum. The posterior end of the lever was attached with a drop of collodion to the upper eyelid near the center of its margin. The anterior end of the lever carried an induction coil resembling the one on the eye. The horizontal and vertical rotations of this coil, detected by a channel of the eye-movement monitor, closely reflected the horizontal and vertical translations of the eyelid. The mechanical loading by this device was so low that subjects became unaware of the attachment after a few blinks.

Six healthy subjects (27 to 56 years old) participated in the experiments after informed consent was obtained. Subjects were seated with the head supported by chin and head rests. Data were collected in a series of trials, each lasting 4–8 s. Either the subject was asked to make several voluntary blinks at self-chosen moments during a trial, or reflex blinks were elicited by air puffs directed towards the eye. To investigate the effects of gaze direction the subjects were instructed to fixate targets corresponding to the primary position and eccentricities of 15° in the four principal directions. However, the primary task of the subject was to generate a number of voluntary blinks, and precision of fixation was not stressed in the instructions. To investigate the effects of prolonged eye closure, subjects were asked to close the eyes and open them again after 1–2 s. Effects of direct mechanical interaction between lids and globe were explored by taping the lids open or closed, or keeping the lids open with a lid retractor.

RESULTS

Blinks initiated with the eye in the primary position

Typical results for voluntary blinks of different sizes, made while the subject was fixating a target straight ahead are shown in Fig. 1. In this condition an initially downward and nasalward motion of the eye was invariably found during a blink. The center of the upper eyelid moved in roughly similar directions. There was a correlation between lid and eye movements in the following respects:

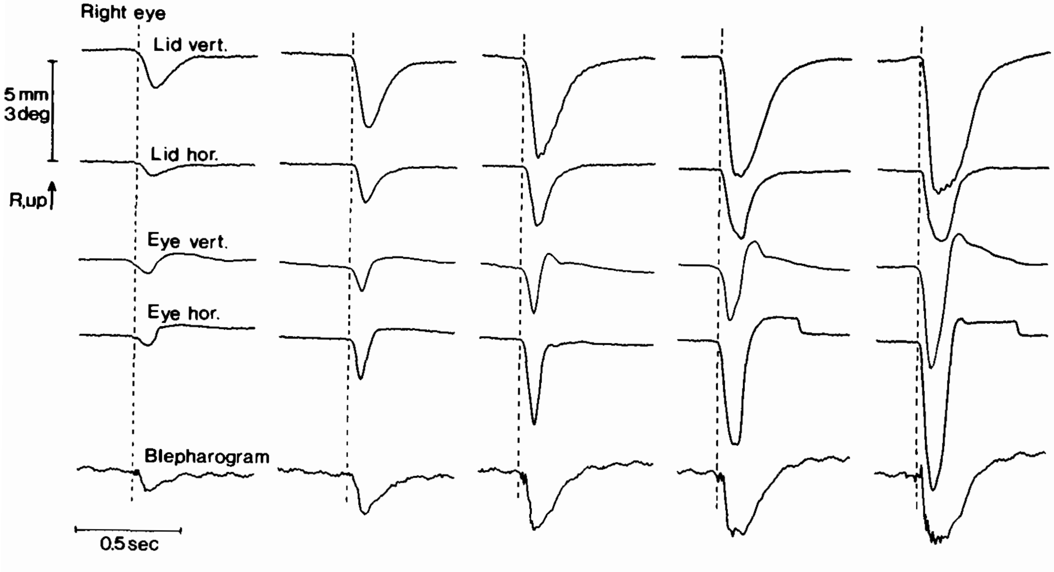

FIG. 1. Vertical (vert.) and horizontal (hor.) lid and eye positions and electroblepharograms recorded during 5 voluntary blinks of increasing magnitude of the right eye of subject HS. Eye movements are scaled in degrees, lid movements in millimeters in this and all following figures. R, right.

1) Both started to move at about the same moment; *2*) both moved initially down and inward; and *3*) larger blinks were associated with larger eye movements. The amplitude of the blink-related eye movements varied between about 1 and 5°. Horizontal and vertical eye-movement components were often of comparable size, but the ratio between them varied considerably between blinks and individuals. The return phase of the eye movement often carried the eye across the original position, with a biphasic eye movement as a result. A corrective saccade usually followed when the end position differed by more than 0.2° from the initial position, indicating the absence of slip of the annulus on the eye. Smaller differences between initial and final eye position were usually not corrected, probably because the subjects were not instructed to fixate very precisely. Lid movements extended maximally about 13 mm vertically and about 3 mm horizontally. They showed no overshoot in the return phase. The return phase of the lid was much slower than the downward phase of the lid and also much slower than the return phase of the eye movement. The linear displacement of the eye (maximally about 5°, corresponding to a lowering of the cornea by 1 mm) was an order of magnitude smaller than that of the lid.

The quantitative relations between the amplitudes of lid and eye movements (first phases, down and inward, only) for blinks of different sizes were determined for two subjects (Table 1). These relations could be reasonably approximated by a linear regression for the vertical as well as the horizontal directions. The calculated linear relations accounted for 63–77% of the variability; the latter seemed to be random, and the data do not suggest that another nonlinear regression would describe their relation any better. The slope for the horizontal eye vs. lid motions (deg/mm) was similar (close to unity) for both subjects. The slopes for the vertical component were very different (1.21 and 0.38); this difference was consistent over two sessions and thus reflects a true difference between subjects.

The electroblepharogram (Fig. 1) showed a reasonably good congruence with the vertical lid movement. The slow components probably reflect the motion of the lid with the electrode over the relatively immobile eye and consist of an "inverted" electrooculogram. The fast components represent the electromyogram of the orbicularis oculi muscle. They are especially marked at the beginning of the blink.

Lid and eye positions together with their velocities (obtained by digital differentiation) are shown for five sequential large blinks in Fig. 2. The lid movement started with a high acceleration and reached a peak velocity up to 280 mm/s within 70 ms. The end position (zero velocity) was reached after ~100–150 ms. The return phase proceeded at much lower velocity (up to ~100 mm/s) and lasted about 300 ms. We confirm earlier observations (7) that the durations of the downward and upward phases of the lid movements are relatively independent of the blink amplitude. The horizontal lid movement was more symmetrical in shape and shorter in duration than the vertical movement; the lid returned sooner to its original horizontal position and often also started to deviate horizontally later. The vertical eye deviation started together with the vertical lid motion and reached maximal velocities of about 75 deg/s. Although there was considerable variation between blinks, on the average, the upward return motion of the eye was about as fast as the downward phase. As a result, the vertical eye movement was completed

TABLE 1. *Relations between amplitudes of initial lid and eye movements*

Subj.	Direction	Mean l (±SD)	Mean e (±SD)	Linear Regression	r^2
HC	Vertical	3.2 ± 0.8	2.6 ± 1.1	$e = 1.21l - 1.25$	0.74
	Horizontal	2.0 ± 0.8	2.3 ± 1.1	$e = 1.09l + 0.09$	0.66
HS	Vertical	6.3 ± 1.3	1.8 ± 0.6	$e = 0.38l - 0.66$	0.77
	Horizontal	3.2 ± 0.8	2.9 ± 1.0	$e = 0.98l - 0.20$	0.63

l, in millimeters; e, in degrees.

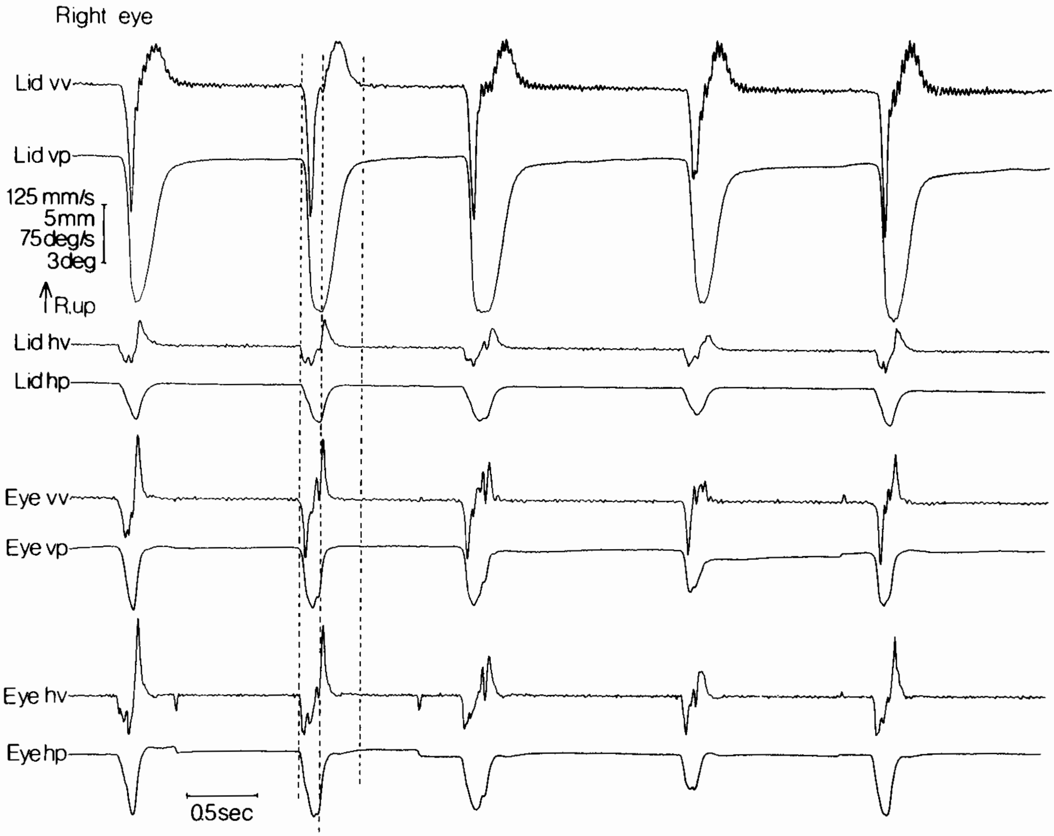

FIG. 2. Lid and eye positions and velocities (derived by digital differentiation) for 5 successive large voluntary blinks recorded from the right eye of subject HS. *Dotted vertical lines* mark the beginning, extreme down position, and end of the vertical lid movement. Oscillations in the vertical lid velocity are due to resonance in the lid transducer; vv, vertical velocity; vp, vertical position; hv, horizontal velocity; hp, horizontal position. R, right.

much sooner (in ~250 ms) than the lid motion, which lasted about 450 ms in these large blinks. The horizontal eye movements showed approximately the same behavior as the vertical eye movements.

Typical two-dimensional trajectories followed simultaneously by the eye and the lid are shown in Fig. 3 for three successive blinks. The scales are in degrees for the eye and in millimeters for the lid; if both were plotted in millimeters of displacement the eye movement would be reduced by a factor 8. The shapes of the eye and lid trajectories were quite different. For the eye movements the horizontal and vertical components were comparable in size, whereas for the lid motion the vertical displacement dominated. The horizontal and vertical motions also showed asynchronies, resulting in curved trajectories and different pathways during the closing and opening phase. Thus, the eye as well as the lid described loops, but these loops went in different directions; as seen by the observer, the right lid of the subject moved clockwise but the right eye moved counterclockwise. Figure 3 also shows clearly that in the opening phase the horizontal lid movement is completed long before the vertical lid movement (cf. Fig. 2).

Although our formal analysis is restricted to voluntary and reflex blinks, the many spontaneous blinks occurring during a session were indistinguishable in shape.

The effect of eccentric gaze positions

Figures 4 and 5 illustrate lid and eye movements during blinks initiated with the eye fixating targets in the primary position

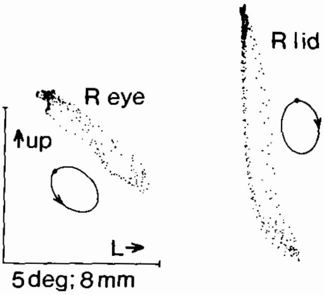

FIG. 3. Two-dimensional trajectories of right upper lid and right eye, recorded simultaneously in three successive large blinks (subject HS). *Ellipses* and *arrows* represent the direction in which the trajectory was followed. R, right; L, left. In this and all following figures, trajectories are plotted as seen by an observer facing the subject.

as well as in secondary positions (15° right, left, up, or down).

The averaged effects of the different gaze positions on the amplitudes of the blink-related eye movements are summarized (for five subjects in which this effect was investigated systematically) in Table 2. The standard deviations represent intersubject variability; within subjects the variability was also considerable (Fig. 5). In the investigated range of gaze (±15°), the first component of the eye movement always remained down and inward. The second component in Table 2 represents the amplitude of the overshoot of the initial gaze position during the return phase.

Vertical eye-movement components were affected only by vertical shifts of gaze, whereas horizontal gaze changes influenced only the horizontal eye movements. The first downward component of the vertical eye movement was slightly enhanced by upward gazing and decreased by downward gazing. The second upward component (overshoot) was considerably enhanced by looking downward except in subject HC, who never showed a second component. Horizontal gaze deviations systematically decreased the inward horizontal component of the blink-related eye movements of the eye gazing in the nasal direction; changes for the eye looking tem-

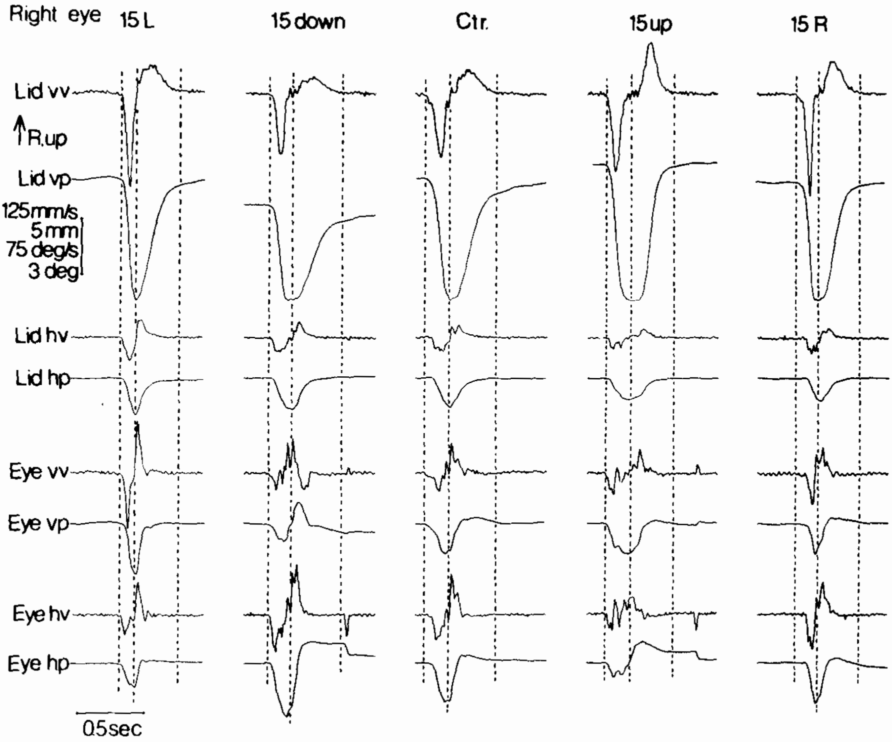

FIG. 4. Representative examples of blinks recorded (in the same session) while the eye fixated centrally (Ctr.) or 15° eccentric in the four principal directions. Subject HS.

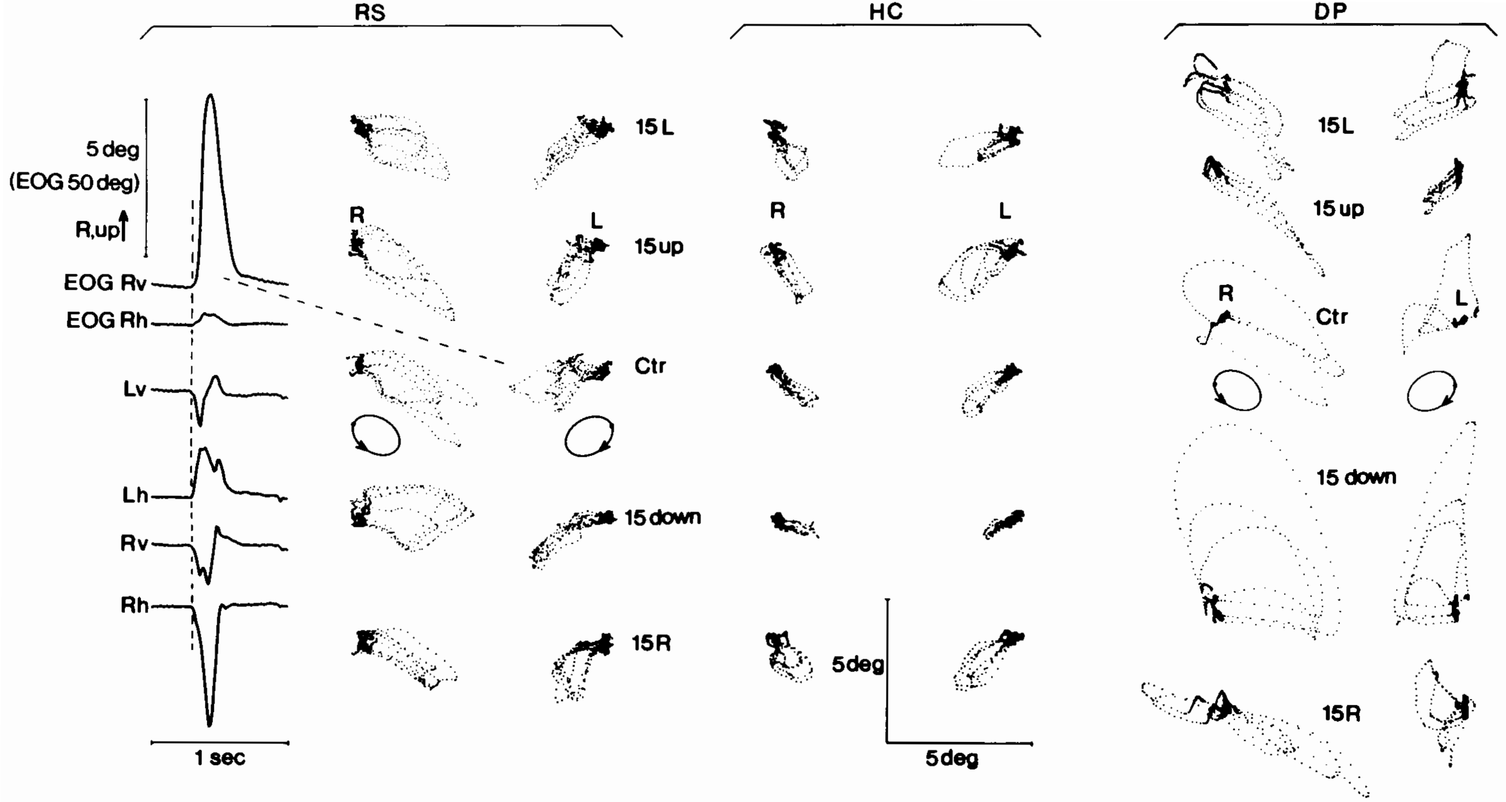

FIG. 5. Two-dimensional trajectories for a number of voluntary blinks, initiated in different gaze positions for right (R) and left (L) eye (recorded simultaneously) in 3 subjects. For subject RS, horizontal (h) and vertical (v) positions of the eyes are also shown as a function of time, for central fixation. The EOG, recorded simultaneously with the coil signals is shown as well; calibration of the EOG traces is 10 × less sensitive.

TABLE 2. *Effect of gaze position on amplitude of first and second components (relative to initial gaze) of biphasic, blink-related eye movements*

Gaze Direction, Components	15° Left	15° Up	Center	15° Down	15° Right
Both eyes					
Vertical I, down	1.9 ± 0.9	1.9 ± 0.8	1.7 ± 0.8	1.1 ± 0.9	1.9 ± 0.9
Vertical II, up	0.4 ± 0.5	0.7 ± 0.7	0.6 ± 0.5	1.7 ± 2.5	0.5 ± 0.5
Right eye					
Horizontal I, left	1.5 ± 0.8	2.4 ± 1.2	2.6 ± 0.9	2.8 ± 1.3	2.6 ± 1.4
Horizontal II, right	0.4 ± 0.5	0.3 ± 0.3	0.3 ± 0.5	0.4 ± 0.6	0.4 ± 0.4
Left eye					
Horizontal I, right	1.8 ± 0.7	1.2 ± 0.5	1.7 ± 0.6	1.8 ± 0.7	1.1 ± 0.5
Horizontal II, left	0.3 ± 0.3	0.3 ± 0.4	0.1 ± 0.2	0.5 ± 0.6	0.4 ± 0.7

Values are means ± SD of 5 subjects. Amplitude in degrees; I, first component; II, second component.

porally varied among subjects and averaged out to virtually zero. There were no systematic changes in the (small) secondary horizontal components. In general, these effects of gaze suggest that in eccentric positions the eye is subject to a pull in the central direction, which accentuates components in that direction and weakens components away from the center.

Vertical gaze position clearly affected the vertical lid motion; since the lid approximately follows the vertical eye position, lid closures starting in an upward position had a larger amplitude than those initiated from a downward position (Fig. 4). The horizontal lid motion was not affected.

Figure 5 also shows an example of the blink EOG (for subject RS), recorded simultaneously with the coil signals. It shows an apparent upward eye movement of >60°, whereas the coil shows a downward motion of ~1.5°. Also the horizontal EOG shows a deviation in the wrong direction. It is clear that the EOG deflections during blinks are artifactual and do not represent eye movements; they may largely reflect lid movements.

Reflex blinks

Reflex blinks were elicited with high reliability by directing a short and not-too-strong puff of air (produced by squeezing a rubber bulb) at the eye. Stronger air streams induced multiple blinks at high frequency or prolonged eye closure. Figure 6 shows typical examples of single voluntary and reflex blinks.

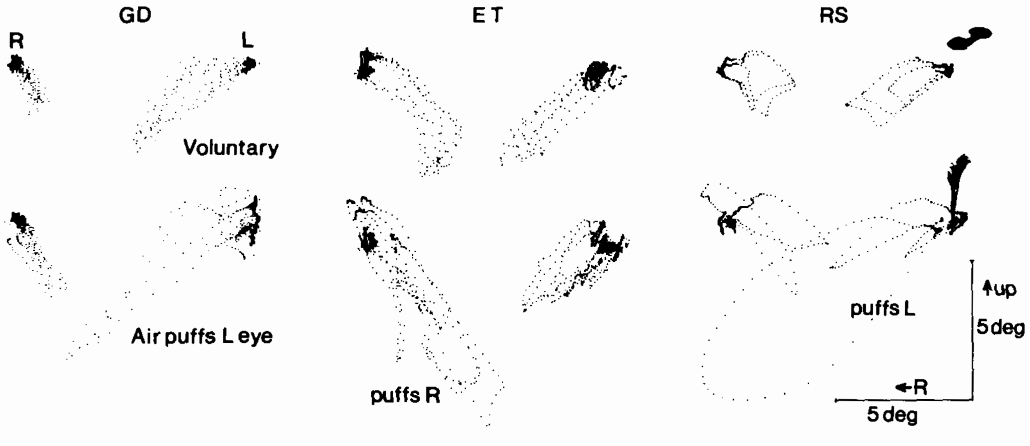

FIG. 6. Comparison of eye movements accompanying voluntary blinks (*top row*) and reflex blinks (*bottom row*) induced in the same session by a puff of air directed at the left eye. The trajectories of 2–3 successive blinks have been superimposed. Three subjects are shown.

The induced blinks tended to be accompanied by larger eye movements (especially of the stimulated eye) than the typical voluntary blinks. However, the shape of the trajectory of the eye was unchanged. Specifically, the external stimulus did not induce any upward motion of the eye. The preferential direction in a loop trajectory (clockwise for the left eye) was maintained also in very large blink-related eye movements (Fig. 6 right side, bottom row).

Effects of keeping one eye closed or opened

One way to distinguish between eye movements generated actively by the extraocular eye muscles and those induced by mechanical interference between the moving lid and the globe is to restrain the lids in a prolonged open or closed condition. As shown in Fig. 7 (compare left and middle columns), the effect of closing one eye with adhesive tape on the trajectory of the eye under the covering lid was insignificant. Neither the shape nor

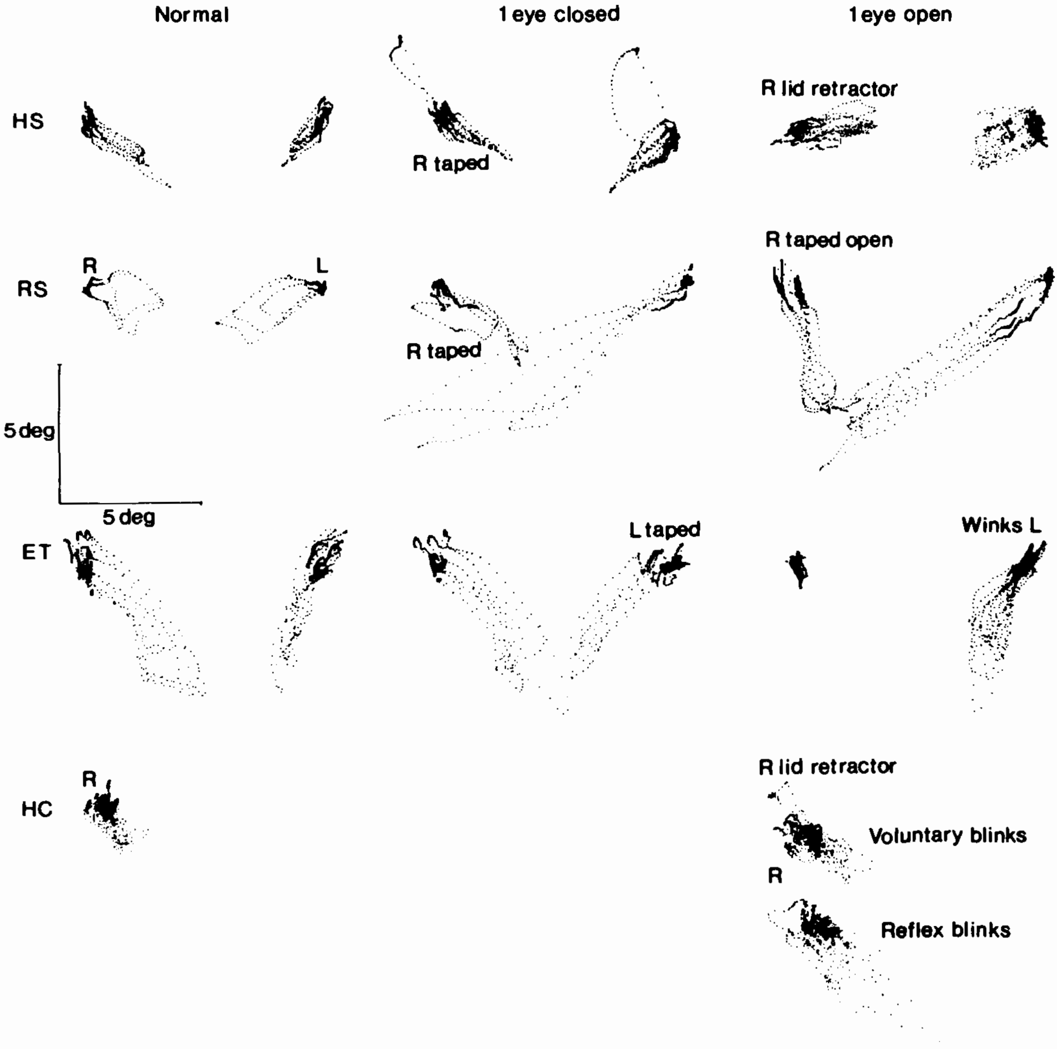

FIG. 7. Effects on blink eye movements of keeping the lids of one eye closed with adhesive tape (*middle column*) or opened (*right column*) by a retractor, tape, or winking of one eye only. *Left column:* normal, unrestrained blinks of one or both eyes recorded simultaneously. Four subjects: HS (*top row*), RS (*second row*), ET (*third row*), HC (*bottom row*). All blinks of one subject were recorded in the same session and initiated voluntarily except those shown in the *lower right diagram*.

the size of the eye movement was essentially different from those observed during normal blinks.

When the lids of the right eye in subject HS were kept open by a surgical retractor, the blink eye movements became somewhat more horizontal but remained approximately of equal size and shape in the right and left eye. The usual downward and inward pattern was restored after removal of the retractor. Blink-associated eye movements in subject HC (Fig. 7, bottom row, right eye only recorded) were directed downwards and inwards before as well as after insertion of the lid retractor. Also reflex blinks in the eye with a retracted lid, induced by a light puff of air, were accompanied by a similarly directed eye movement, although as usual the amplitude was larger than for voluntary blinks (cf. Fig. 6).

Also when one lid was kept open by adhesive tape, large blink-related eye movements were still recorded, as illustrated in Fig. 7, for subject RS. These findings, taken together, suggest that the eye movements during blinking are not generated by the sliding of the lid across the eye.

Subject ET was able to blink with the left eye only (wink), without moving the right eyelid. As shown in Fig. 7, this produced the usual blink-associated eye movement in the winking eye, but none in the right eye. This shows that it is possible to activate the blinking mechanism of one eye only without activating either lid or eye motion in the other eye.

Velocity and duration of blink eye movements and saccades

For a number of blinks, obtained in one session (subject HS), the duration and maximal velocity of the vertical eye movements was calculated for the downward (motion from initial to lowest position) and upward phase (motion from lowest to highest position) separately. In Fig. 8 these are plotted as a function of eye-movement amplitude for the two eyes (crosses, downward phase; dots, upward phase). The left half of the figure shows the relation for normal conditions, with both eyes open. The diagrams for right and left eye are similar. The distribution of duration and velocities for the upward and downward phase overlap a great deal,

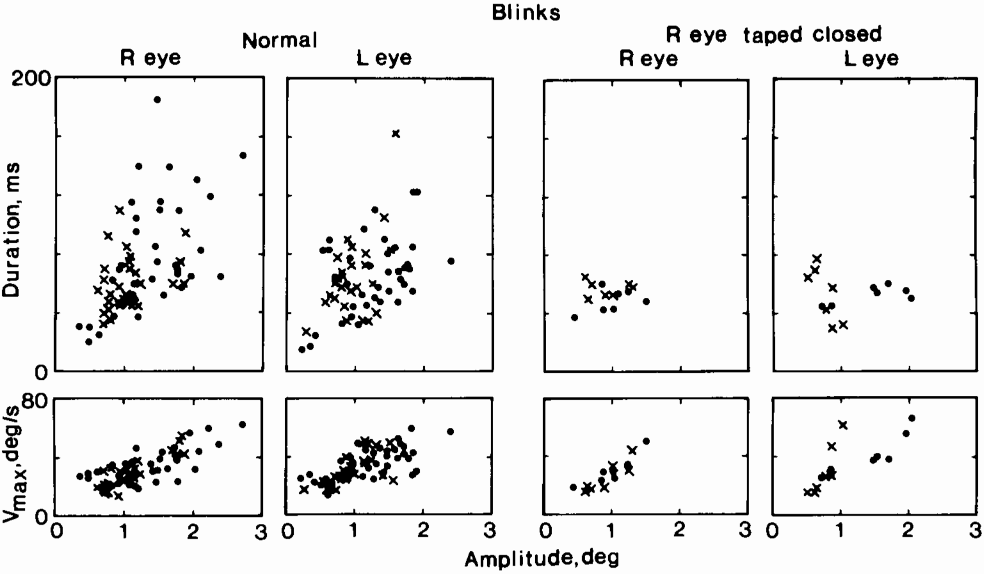

FIG. 8. Duration and maximal velocity of the downward (*crosses*) and upward (*dots*) movements of blink-associated eye movements, as a function of amplitude. Subject HS. Data for left and right eye were recorded simultaneously. *Left two diagrams* show data obtained with both eyes and lids moving freely. *Right two diagrams* were obtained in the same session after closing the right eye lids with adhesive tape.

but the upward phases were generally somewhat larger, due to the occurrence of overshoot. Maximal velocity as well as duration were approximately proportional to the amplitude of the eye movement. For a 2° eye movement the duration and maximal velocity were ~100 ms and 40 deg/s, respectively. The right side of Fig. 8 illustrates the same relations obtained for blinks while the right eye was closed with adhesive tape. The only clear effect of this closure seemed to be that the upward motion of the eye was now equal in amplitude to the downward motion; otherwise the velocity-duration-amplitude relations of the closed right eye were similar to those in the uncovered left eye and uncovered right eye. In all cases, there was considerable scatter of the data points.

A similar comparison was made (Fig. 9) for voluntary vertical saccades in the downward (crosses) and upward direction (dots). With both eyes open, the relations were equal for the two eyes (Fig. 9, upper half) and in approximate agreement with the literature for horizontal saccades (24). For 2° saccades the duration and maximal velocity were ~40 ms and 60 deg/s. Thus, saccades are shorter and faster than blink-related eye movements. Closure of the right lids with adhesive tape (Fig. 9, lower half) did not change these

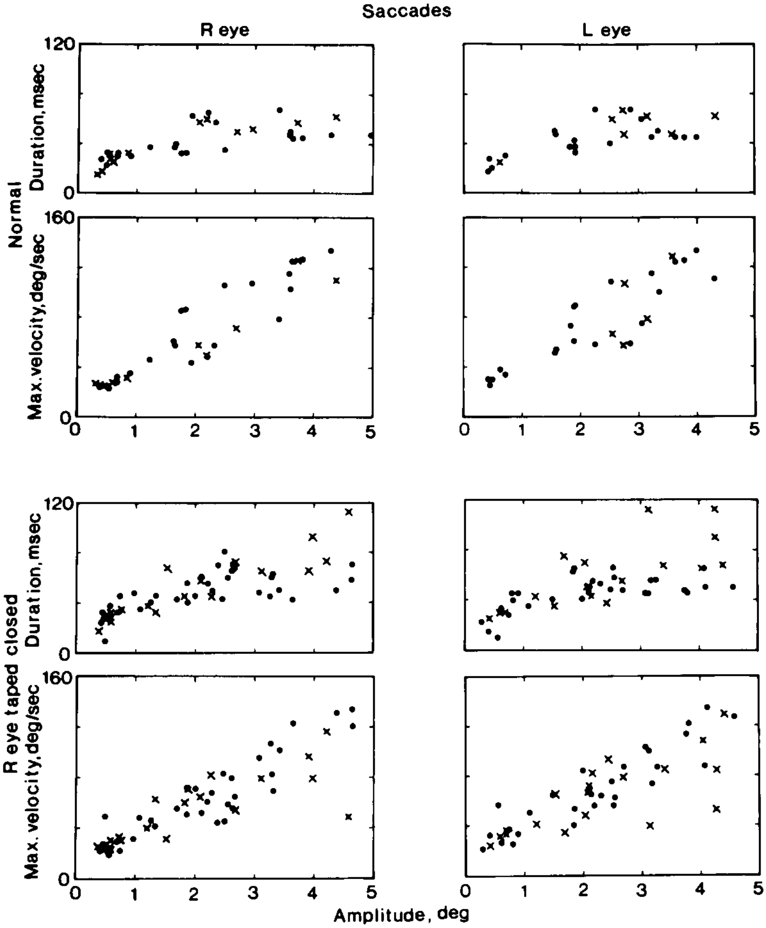

FIG. 9. Duration and maximal velocity of a sample of downward (*crosses*) and upward (*dots*) vertical saccades, as a function of their amplitude. Saccades were simultaneously recorded in the right and left eye in subject HS. *Upper diagrams* represent saccades recorded with both eyes normally open; *lower diagrams* show the relations for saccades made with the left eye normally open but the right eye lids closed with adhesive tape.

relations at all; the saccades of the closed right eye were as fast and short as the ones executed simultaneously with the open left eye or the ones made with the right eye opened. These findings show that blink-related eye movements are not saccadic; they also demonstrate that a closed lid does not noticeably change the shape of either blink eye movements or saccades. This argues against any significant mechanical coupling between the lid and the globe. It also shows that the annulus, even when covered by the eyelid, does not alter the characteristics of eye movements.

Eye movements during prolonged lid closure

The eye movements associated with long voluntary closures of the lids were entirely different from those occurring during blinks. Typical examples of lid closures lasting about 2 s, with the eye initially in the primary position, are shown in Fig. 10. These may be compared with the recordings of blinks in Fig. 2 and 4, recorded from the same subject. The closing movement of the lid was in general slower than during a blink, with a maximum velocity up to ~125 mm/s, less than half the maximum velocity during blinks. During the downward lid motion the eye showed a small, transient downward movement, but this was followed by a slow and tonic deviation, which was upward in the subject (HS) illustrated in Fig. 10. This motion was not faster than about 20–30 deg/s and gradually slowed down to reach an end position after 0.5–2 s. In the opening phase, the lid motion was approximately the mirror image of that in the closing phase. However, this was not the case for the eye movement. The return motion of the eye (downward in Fig. 10) was much faster than the initial deviation, started before the lid opening, and

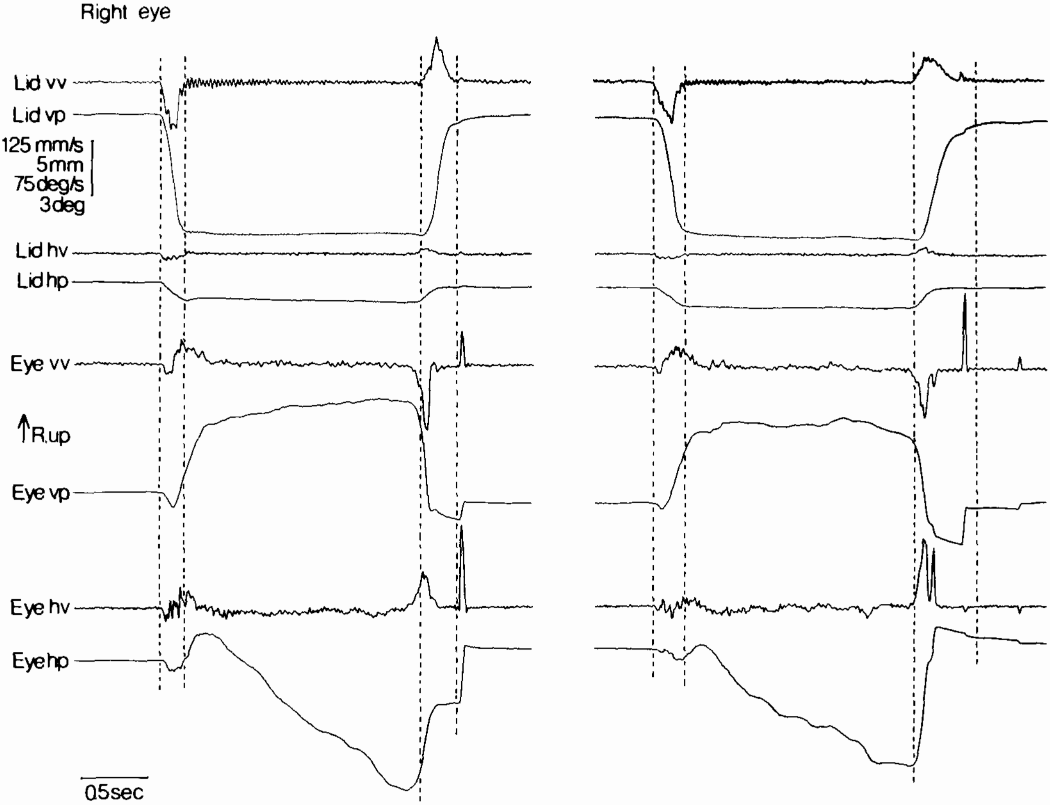

FIG. 10. Position and velocity of the right upper lid and eye of subject HS during two prolonged eye closures. The initial gaze direction corresponded to the primary position of the eye. Lid motion scaled in millimeters; eye motion in degrees; vv: vertical velocity; vp: vertical position; hv: horizontal velocity; hp: horizontal position.

was completed much earlier than the lid opening. Often it did not return the eye exactly to the previous gaze position, which was then reached by a subsequent saccade after restoration of vision. The tonic deviation contained a significant horizontal component as well, which was predominantly inward in subject HS but consisted of several phases and was rather variable between trials. The vertical component had a characteristic shape in each subject. It was not the result of ocular drift in the absence of a fixation point: *1*) Its initial velocity was much higher than dark drift, and *2*) dark drift was sometimes seen superimposed on the tonic deviation. In the case of subject HS, the dark drift was downward; when it occurred, the elevated eye continuously drifted down and was reset in the upward direction by saccades (not illustrated).

Tonic elevation, in agreement with Bell's description, was not found in all cases. All our six subjects showed a tonic vertical deviation; in three it was consistently upward, and in three downward. The horizontal motions were rather variable between trials and subjects. The artifactual nature of EOG recordings persisted during prolonged eye closure, and indicated elevations up to 70° even when the coil signals demonstrated a depression.

The size of the vertical tonic deviation varied between 5 and 20° between subjects and was also clearly affected by the initial vertical gaze angle. This is shown for subject HS in Fig. 11, recorded in the same session

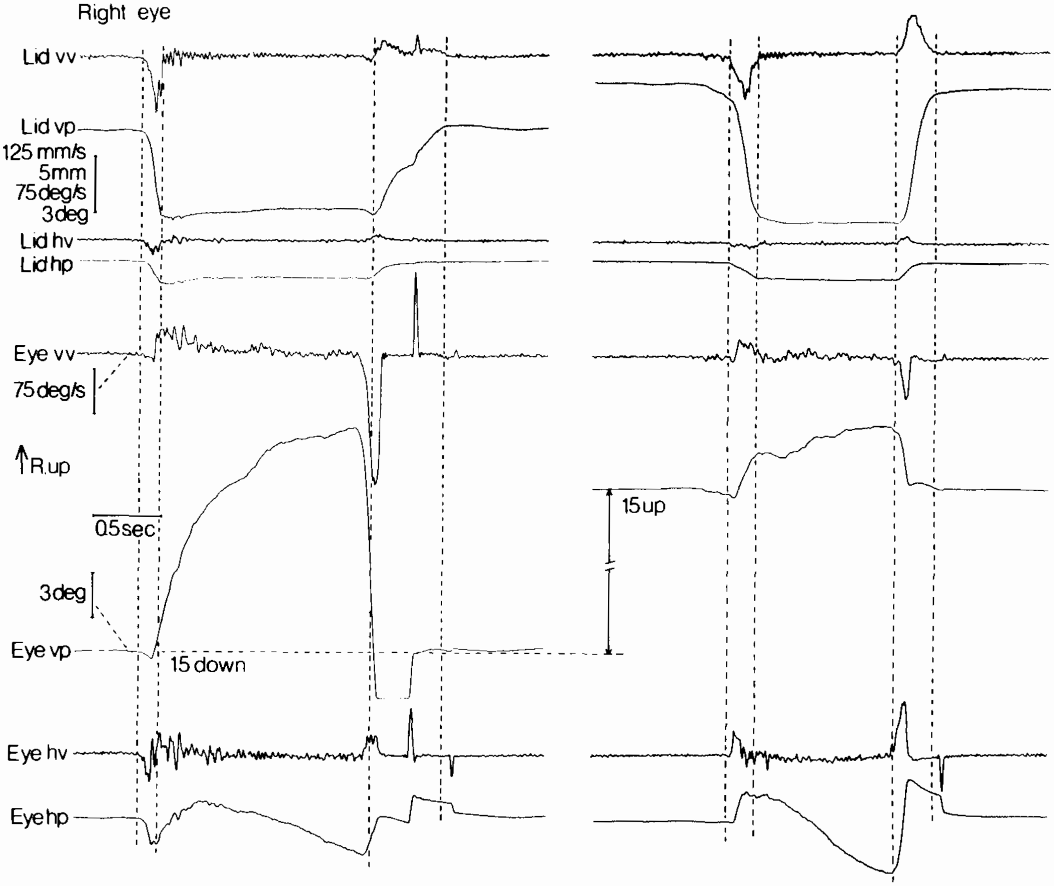

FIG. 11. Position and velocity of the right upper lid and eye of subject HS during two prolonged eye closures, initiated with the gaze directed 15° down (*left graphs*) and 15° up (*right graphs*). In the *left graphs*, the size of the vertical eye motion necessitated plotting at a lower sensitivity (see separate *calibration bar*, valid for this curve only). Even so, the lowest position during the return movement of the eye was truncated due to saturation of the monitor.

as Fig. 10. When the gaze direction was initially 15° down, the tonic elevation was enhanced, whereas it was decreased when the eye started in a 15° up position. However, these changes were much too small to compensate for the initial offsets of gaze. From the primary position the eye moved upward about 6° (Fig. 10), from the 15° down position it was elevated by about 15°, and from the 15° up position by about 3° (Fig. 11). Thus, the tonic elevation did not carry the eye to a constant end position in the orbit.

Finally, prolonged eye closure was also tested in the sessions in which the right eyelids in subjects HS and HC were kept open by a retractor, the effect of which on blinks was discussed previously (Fig. 7). The habitual (Fig. 10) conjugated upward ocular deviation that occurred in subject HS during voluntary eye closure was unchanged after insertion of the retractor. Under unrestrained conditions, subject HC produced downward eye movements (Fig. 12, left column). Interestingly, with the lids restrained in the open position this pattern changed into a consistent ocular elevation during attempted lid closure. After removal of the retractor (Fig. 12, right column) the downward motion returned. This suggests that elevation (the classical Bell phenomenon) is more prone to occur when normal lid closure is prevented.

It is remarkable that these tonic deviations of the eyes occurred even though the artificially opened eye had every opportunity to fixate the usual central fixation mark. During these attempted closures the subjects had a vague notion that their gaze shifted upwards. Apparently, the neural commands associated with eye closure tend to disrupt the habitual tendency to maintain fixation.

DISCUSSION

By use of the scleral coil technique, we have recorded consistent transient downward

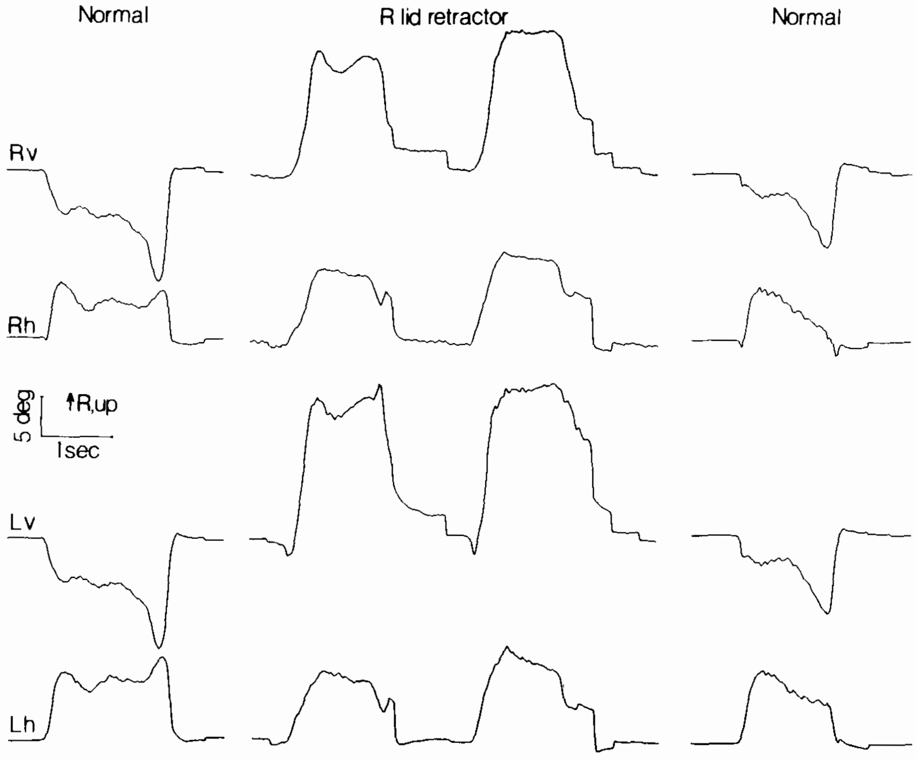

FIG. 12. Vertical (v) and horizontal (h) position of left (L) and right (R) eye recorded simultaneously in subject HC during prolonged eye closure with both eyes unrestrained (normal; *left graphs*) and with the right eye lids held open by a retractor (*middle graphs*). *Right graphs* were recorded after removal of the lid retractor. The eye of HC showed depression in the unrestrained condition, but elevation while the lids were restrained in the open position.

and inward eye movements during rapid blinks, whereas prolonged eye closure proved to be associated with slower, tonic, vertical deviations that could be either upward or downward. Our findings for blink-associated eye movements are obviously at variance with the classical notion of an upward eye movement, introduced by Bell (3) on the basis of what seems nowadays weak and circumstantial evidence, but, nevertheless, propagated ever since in the neurological literature. None of the evidence in the literature for upward eye motion during blinks seems acceptable by current standards because the instrumentation was inadequate.

A remarkable exception is the psychophysical work by Ginsborg and Maurice (9) who studied the apparent transient deflections from the straight trajectory of an oscilloscope spot during small saccades and blinks. Although their notes on blinks are extremely short, they state that the eyes "rotate toward the primary position at the beginning of the blink," and that "there is a position of the eye, looking slightly downward and about 10° inward, from which no marked deviation of the trace occurs." This seems to suggest that the latter position was the "primary position," and that from a straight-ahead position the eyes would rotate downward and inward. Recent measurements by Volkmann et al. (21) have confirmed the occurrence of small downward and inward eye movements during blinks by a similar technique, and also by objective eye-position recordings with a double Purkinje image tracker (which obviously records only the initial stage of the blink).

These transient eye movements could originate either from active contraction of the extraocular muscles, from the sliding action of the lids across the eye, or from pressure exerted upon the globe by the contracting orbicularis oculi muscle. The corneal bulge offers some potential leverage for the descending eye lid, and since there is some superficial resemblance between the directions of lid and eye movements, a contribution from such a mechanical coupling cannot be entirely discounted. Its contribution, if any, seems small in view of the minimal effects of artificial fixation of the lids in the open or closed condition (Fig. 7). Although the scleral annulus might theoretically change the amount of coupling between lids and eye, the absence of any overt effect of permanent lid closure in one eye on either blink eye movements or saccades (Figs. 8 and 9) does not support this possibility. Insertion of the coil with the lead wire in the temporal instead of the (usually preferred) nasal canthus did not alter the characteristics of the blink eye movements either.

Patients with a unilateral facial nerve paralysis would offer a possibility for a future assessment of the contribution of the orbicularis oculi muscle (including any pressure effects) to blink eye movements. We made a conservative attempt to induce a temporary block of the nerves innervating the orbicularis oculi by local anesthesia in two of our subjects, but were unsuccessful, probably because of the wide ramifications of these motor nerves.

On the other hand, the possibility that the blink eye movements are generated by activity of the extraocular muscles seems very real. The fact that the eye and the lids follow distinctly different trajectories in space (Fig. 3) and time (Figs. 2 and 4) points in this direction. More significantly, considerable retraction (0.7–1.6 mm) of the human eyeball during blinks has been reported (6, 7). Such a retraction, observed even with the lids taped open and away from the eye (7), is most probably generated by a cocontraction of the extraocular muscles, with a slight concomitant ocular rotation as a secondary and physiologically meaningless phenomenon. In the rabbit, a vigorous burst of activity occurring simultaneously in the superior and inferior rectus muscle has been recorded during blinking (7) in direct support of this mechanism. In this light the rotatory component of the blink eye movement could, as an epiphenomenon, have various directions and trajectories depending on the resultant of the muscular actions, although motion to a similar position of equilibrium from various gaze positions would seem likely. The retraction of the eye during blinks appears to be a universal phenomenon (7) found in animals without (fish, human) and with (rabbit, guinea pig) a retractor bulbi muscle. The blink-associated rotatory eye movements, recorded with a search coil, are upward and abducting in the rabbit and guinea pig (7) and absent in the monkey (19). Incidentally, these findings argue against a simple mechanical coupling between the lid and the eye. Rapid blinks can be easily combined with saccadic gaze shifts. In some patients (23) blinks even facilitate the generation of saccades with normal velocity, a finding that supports the activation of extraocular muscles during blinks.

Our findings disagree in some respects with those of Allik et al. (1), obtained with a modified magnetic induction method in which a metal annulus, without a lead, is mounted on the eye. Current induced in this ring generates a secondary magnetic field, the orientation of which is detected by sensor coils. Somewhat similar leadless systems have been described by others (4, 17). Although the use of an annulus without a lead has distinct advantages, such as increased comfort and elimination of malfunction due to broken leads, other problems are introduced such as considerable nonlinearity and sensitivity to translation. The possibility may have to be considered that the upward eye movements during blinks recorded by Allik et al. (1) reflect the retraction of the eye rather than a true rotation, especially since the time course of their blink-related eye movements (their Fig. 3) resembles the one described for eye retraction (6, 7). This time course (especially the return phase) is slow, similar to that of the lid motion, whereas the time course of blink-related eye movements in our recordings is much faster than of the lid motion. Allik et al. (1) also reported considerable slowing of saccades by the closing of both eyes. Because closing of one eye in our experiments did not affect saccadic parameters, this phenomenon must be due to changes in the central programming and not to peripheral mechanical effects of the closed lids.

Prolonged voluntary closure of both eyes induces a slow, tonic deviation of the eye with an entirely different time course than found during blinks. These findings are more in agreement with the traditional views, except that a consistent upward motion was found in only three of the six subjects, the other ones moved the eyes downward. Remarkably, the depression during unrestrained voluntary closure was converted into unambiguous, large elevation after the insertion of a lid retractor in subject HC. This observation may be of importance in the interpretation of classical findings, which have all been obtained in subjects with impaired lid closure or by manual restraint of the lids. The largest number of observations of this type was probably collected by Hall (10) who examined the eye deviation during attempted lid closure, with the upper lid of one eye manually fixed, in no less than 1,250 normal people. He found maximal upward movement in about 60%, medium upward movement in about 30%, and absence of upward movement (including a small number of cases with downward motion) in about 10% of his sample. Hall (10) also observed one case of a unilateral facial paralysis in which attempted lid closure resulted in an extreme downward and inward motion of the affected eye (without manipulation of the lids), and he mentions earlier observations of a similarly inverted Bell's phenomenon. Our findings (which should be confirmed in a larger sample of subjects) suggest that during unrestrained voluntary lid closure depression of the eye occurs as often as elevation, but that the latter may prevail whenever normal lid motion is impossible.

The dynamics of the eye and lid motion in our recordings agree with Hall's (10) description. The lids close first (palpebral phase), after which the eye deviates slowly (global phase). In the opening phase, the eye starts returning towards the primary position before the beginning of the lid opening. This sequence of events was also recorded by Allik et al. (1). However, our observations on the effect of initial gaze position do not support their findings of a constant end position of the globe. As Allik et al. (1) discuss, such constancy is relative in any case, since a subject is perfectly able to move his eyes in any planned direction once the eye is closed.

Finally, our observations corroborate earlier reports (2, 13, 19) that the EOG is totally unsuitable for recording eye movements in combination with lid movements; the EOG deflections during lid closure in no way correspond to the true eye motions recorded with the scleral coil. As lid movements are associated with all vertical eye movements, this implies that all vertical EOG recordings, even without blinks, are highly contaminated by changes in lid position and therefore essentially unreliable as an eye-position monitor.

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