

Blink-Related Eye Movements

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Eye movements that accompany a blink have been measured in human subjects by the use of a visual-persistence method. With straight-ahead binocular viewing, each eye typically rotates nasalward and downward 1–2 deg during the closing phase of a blink. These eye movements are more rapid than the lid movements as recorded by high-speed photography. In fact, the eyes have already completed their initial rotation and started back again before the lids are fully closed. With off-center viewing, a blink causes each eye to rotate toward its primary position of regard. Indeed, if the eye is already in that position when the blink starts, the eye moves very little. With eyelids taped open, an eye tracker can be used, and records confirming the visual persistence tracings are obtained. Sequential photography of the cornea in profile reveals that the eye moves inward and back out again during a blink. The amplitude of this retraction is typically less than 1 mm; and its time course, slower than that of the rotational eye movements, parallels the closure and opening of the lids. In normal conditions of viewing there is no evidence of conjugate saccades, or of any large, upward rotation of the eyes (Bell's phenomenon) that was once believed to take place during a blink. *Invest Ophthalmol Vis Sci* 28:334–342, 1987

There is widespread disagreement in the older literature^{1–5} about the amplitude and the time course of eye movements that occur during a blink. There appear to be two main reasons for this confusion: (1) The various methods for measuring eye movements are either not sufficiently sensitive, or subject to extensive interference when the lids close over the eye, and (2) there is wide variation in the eye movements themselves, depending on the direction of gaze and the amplitude of the blink.

The aim of the present research is to measure blink-related eye movements by the use of a simple and direct method.⁶ The method is a subjective one, but it results in eye movement traces, the reliability of which is confirmed by control experiments on the double Purkinje image eye tracker.⁷ We confirm reports^{6,8–10} that with normal binocular viewing, each eye typically rotates nasalward and downward 1–2 deg at the outset of a blink. We then proceed to compare the time course of these eye movements to photographic records of the opening and closing of the lids. In further photographic recording, we have obtained simultaneous photographic records of the retraction of the globe and closure of the lids. Finally, we consider the possibility that the eye movements that we have observed to accompany a blink can account for the visual suppression that is known to accompany a blink.¹¹

Materials and Methods

Of the various procedures for the objective recording of eye movements, the electro-oculogram and the method of corneal reflection are insufficiently sensitive to measure the eye movements of interest to us here. Adequate sensitivity could doubtless be provided by a plane mirror or a search coil device attached to the eye or by a Purkinje image eye tracker. Any attachment to the human eye adheres by surface tension to the mucous conjunctiva. Relatively little slip occurs when the attached device is used to measure small movements of an open eye, but a lid artifact of unknown amplitude may occur when the upper lid sweeps down over it during a blink. And a normal blink will also destabilize an eye tracker when first the lashes and then the upper lids occlude the infrared beam that is used to plot eye movements. We have therefore chosen a subjective method to measure the eye movements during a blink. The method is the one outlined in 1959 by Ginsborg and Maurice.⁶ By using a calibrated measuring screen and choosing an appropriate light spot, we have aided the subject in making accurate, high-resolution tracings of the eye movements that accompany a blink. Four human subjects (the authors) gave informed consent.

Figure 1 is a diagram of the apparatus. A mirror is attached to the shaft of a synchronous motor. A projector is used to focus a small, intense spot of light reflected from the mirror to a screen. As the mirror rotates, the spot flies across the screen at a constant speed of 25.3 deg/sec as seen by the observer's eye. The subjective appearance, in a suitably darkened room, is that of a straight streak of light representing the mo-

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mentary persistence of vision as the spot traverses the field seen by the stationary eye. The screen itself is 167 cm from the eyes. It is a matte white square 50 cm × 50 cm. It presents a grid of fine black lines and a small, stationary point to facilitate fixation and measurement.

Eye Movement Tracing

The subject learns to fixate steadily upon the stationary point and to execute a blink just as the spot of light is flying past it. A successful observation is one in which any eye movement occurring at this time shows up as a deflection of the line of light from its otherwise straight trajectory. The time course and amplitude of the deflection can be described by the subject in terms of its appearance against the measuring grid. An upward deflection of the horizontally flying spot indicates a downward eye movement; a rightward deflection of the vertically flying spot indicates a leftward eye movement. With a little practice, the subject learns to use a clipboard to facilitate tracing out the apparent course of these components on a piece of graph paper that represents the Cartesian grid of the screen. A gap appears on any trace in which the blink is of sufficient amplitude to obscure the pupil. The length of the gap denotes the duration of occlusion of the pupil by the lids.

Calibration of the system is in terms of visual angle through which the eye must have rotated, as indicated by each square of the grid, in the direction orthogonal to that of the flying spot, and in terms of time per unit square in the direction of the spot. Care is taken to compensate for the eye's own movement in this direction. This is done by having the subject make one set of observations in which the spot is moving from right to left, and another set from left to right. The mean time course of the two traces can then be taken as a true estimate of the vertical component of the movement during the blink. Similarly, two sets of traces are obtained in order to estimate the true horizontal component from upward and downward spot movements.

Records of eye movements such as those that appear in Figures 2-5 are corrected reproductions of the subjects' tracings of the appearance of the trajectories of the spot of light. The major correction is for the optical reversal of direction, such that an upward tracing by the subject indicates a downward movement of the eye. A minor correction was done by the averaging, just mentioned, of tracings made from the two opposite directions of the excursions of the light spot.

Preliminary observations immediately revealed that movements of the eye during a blink are typically of moderate amplitude (0.5-1.5 deg vertically and 0-0.5 deg horizontally) and speed (50-75 deg/sec vertically

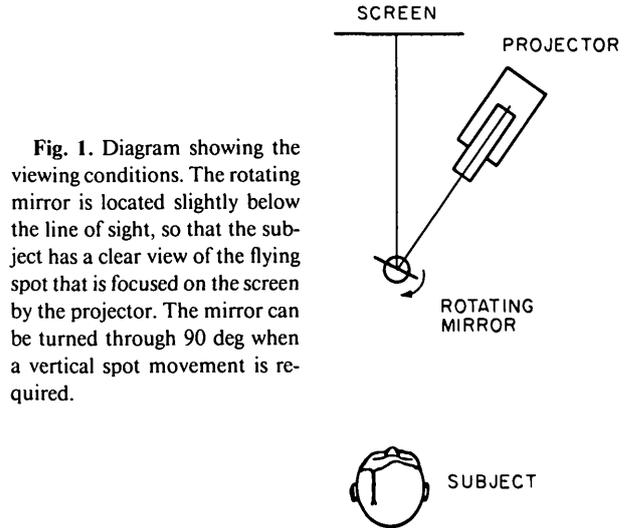


Fig. 1. Diagram showing the viewing conditions. The rotating mirror is located slightly below the line of sight, so that the subject has a clear view of the flying spot that is focused on the screen by the projector. The mirror can be turned through 90 deg when a vertical spot movement is required.

and 40 deg/sec horizontally). These estimates hold for three subjects with "straight-ahead" viewing. But when the head position is changed, so that the subject must view the fixation point by looking off to the left, right, up, or down from the position "straight-ahead," there are significant changes in the eye movements that accompany a blink. To explore this effect more fully, we constructed a combination of chin cup and forehead rest that was calibrated in 10-deg steps for head orientations that were to the left, right, up, or down from the subject's preferred "straight-ahead" position of gaze. Observations were then conducted with a "sta-

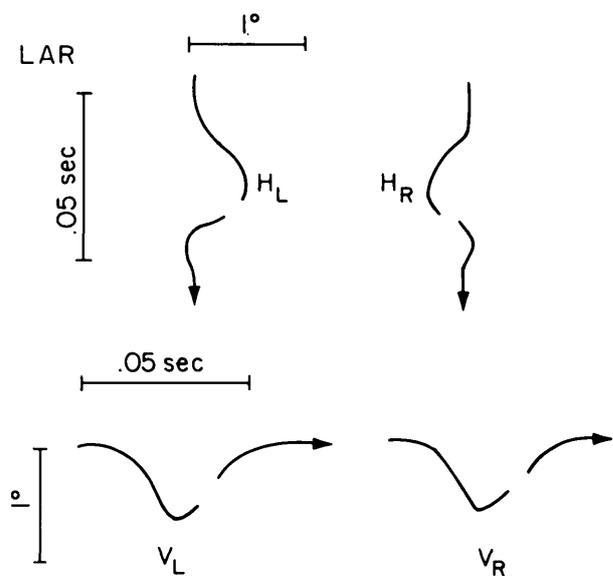


Fig. 2. Sample records obtained with the flying-spot procedure showing the horizontal (H) and vertical (V) components of the left-eye (L) and right-eye (R) movements at the time of a blink. In each record time, in the direction of the arrow, is scaled as indicated by the 0.05-sec line. Eye movement amplitude is scaled by the 1.0-deg line.

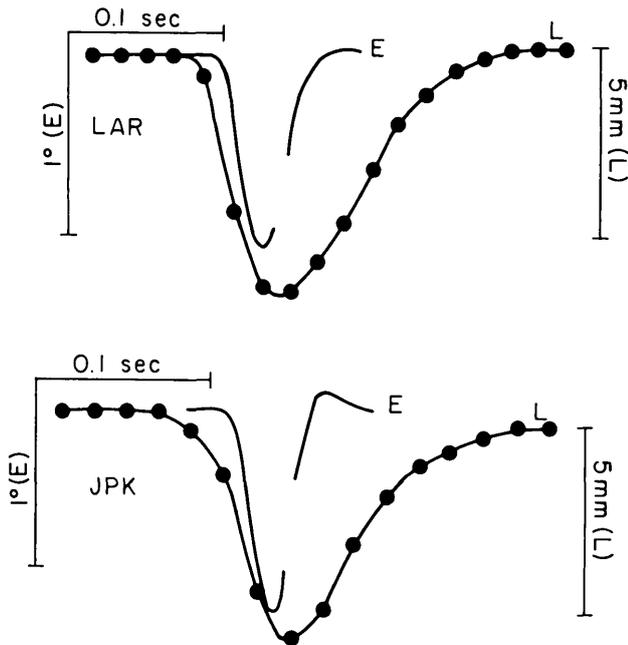


Fig. 3. Time courses compared for the vertical components of movement of the eyeball (E) and the upper lid (L) during a voluntary blink of moderate strength. Vision is occluded (as shown by the gap in the eye movement trace) when the lid reaches its lowest position. Right eye, monocular viewing.

tionary spot" method replacing that of the "moving spot" for studying eye movements induced by a blink. This method has the advantage that no special timing is required, and any eye movement results in an after-image being painted across the retina. The subject could thus observe the apparent deflection of the light spot and estimate the total amplitude and direction of eye movement accompanying the blink, even though the

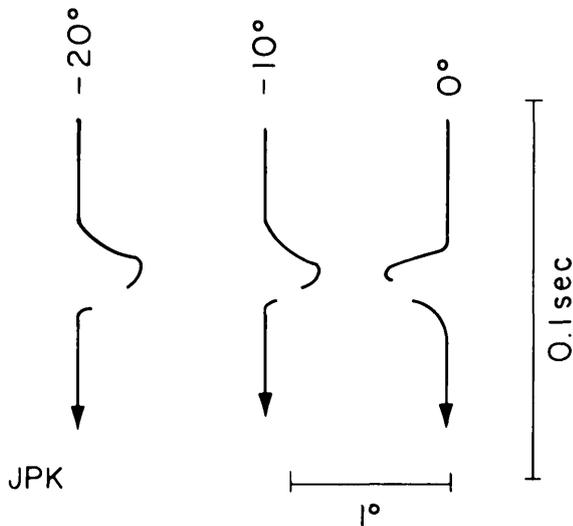


Fig. 4. The horizontal component of eye movements during a blink. In the primary (0 deg) gaze position the right eye moves left (nasalward). With other directions of gaze the blink results in an eye movement toward the primary position.

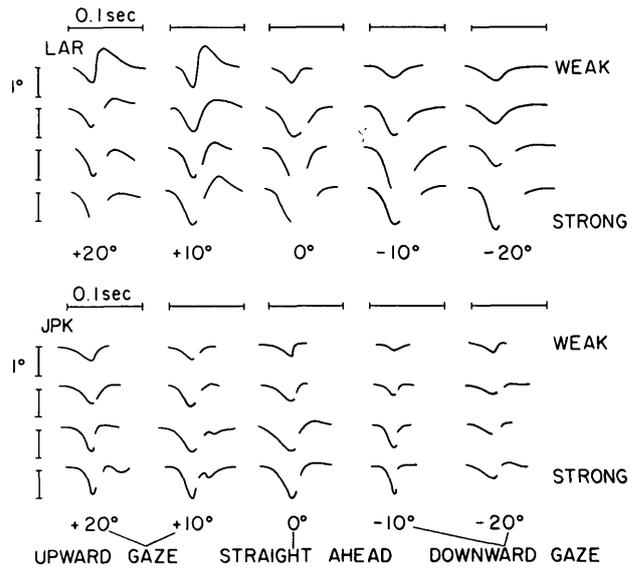


Fig. 5. Series of eye movement records showing the effects of voluntarily increasing the strength of blink (top to bottom) and shifting the gaze from upward to downward directions (left to right). Right eye viewing, subjects LAR and JPK.

dynamic information yielded by the moving-spot procedure was no longer obtained. It is also true that the largest blinks involve a brief interval during which the upper lid completely covers the pupil; thus a small segment of eye movement is missing. But it is clear from the tracings by the moving-spot method that the entire amplitude of eye movement is revealed prior to lid closure.

A somewhat indirect procedure for recording the eye movements that accompany a large blink is to restrain the lids of one eye, thus preventing them from getting in the way of eye movement recording. The voluntary blinks of normal subjects show that the lid motions of left and right eyes are well synchronized; and binocular observations of the accompanying eye movements have confirmed that they, too, are synchronous. The idea is to ask the subject to blink as normally as possible, so that the left eye executes a typical blink and the right eye, subject to the same command, will carry out whatever eye movement results from the extraocular muscles rather than from the passive forces exerted by the lids, since now they are held open. In practice, however, this seemingly simple procedure is difficult for some of our subjects to carry out. Particularly irritating for them was the drying of the corneal surface that took place during any interval of time that was sufficient for eye movement records to be obtained. This was not true, however, for other subjects who felt little or no discomfort due to holding open the lids.

Lid restraint can be done with the fingers, but some subjects tolerate a more systematic procedure of taping

the lids apart. For the upper lid, a piece of tape (Dermiclear, Johnson and Johnson Products, Inc., New Brunswick, NJ) is attached near the margin of the center, and the free end is pulled up and anchored to the forehead. The lower lid is similarly pulled away from the globe, the tape being anchored to the cheek below it. This works best with lids that are relatively large and loose. The subject then appears to execute a normal blink with the left eye, but the right remains sufficiently open for continuous recording of the eye movements. Records have then been obtained not only with the moving and stationary spot techniques but also with the eye tracker.

Eye Tracker Recording

An eye tracker (SRI double Purkinje image device⁷, SRI International, Menlo Park, CA) was used for control experiments in which the lids were taped out of the way. The eye tracker trials were of particular interest because they provided a highly sensitive and objective record of eye movements at the time of the blink. The results could then be compared with those of the subjective method with the same subject under conditions as nearly as possible the same with respect to head orientation, eye fixation, and lid restraint. These trials were completely successful for only one of our subjects, KAM.

During the tracker runs, the subject was seated comfortably and the head was held steady by a dental impression bite bar and forehead rest. A black patch covered the left eye in order to facilitate monocular fixation, but the presence or absence of such a patch has little effect upon records of eye movements during a blink. The subject viewed a large, grey, circular field with her right eye through a Maxwellian view optical system. A white dot that subtended 5 min of visual angle was centered in the field and was the fixation target.

The subject's blinks were recorded with a pair of cup skin electrodes (Grass Instrument Co., Quincy, MA) filled with electrode cream (EC₂, Grass) and applied above and below the left eye to provide the signal that we have called an electroblepharogram (EBG).¹¹ The leads from these electrodes provided the input to a differential amplifier (Model 113, PAR) where the signal was amplified and filtered (1 Hz, 30 Hz). A third electrode clipped to the ear lobe was grounded at the amplifier. The resulting signal was monitored on an oscilloscope and recorded during eye movement data collection. Subjects readily learned to vary the extent of their voluntary blinks. Blink amplitude can be monitored by EBG recording or by reference to the visual tracings such as those in Figure 5.

Eye position and the EBG were digitized at 250 HZ by a MINC 11/23 computer and stored on disk for

later analysis. A VT125 graphics terminal and slaved bit map graphics printer were used to plot figures. Eye movement records from a series of blink trials were averaged by superimposing data (ie, adding together digitized records) aligned in time to the peak of the blink EBG. Each two-dimensional figure (see Fig. 10) is the average of 10 similar blink trials. This system has a minimum angle of resolution less than 2 arc-min.

The first trial of each session was for calibration. The subject fixated the central fixation target and then saccaded to follow the step movement of the target 2 deg upward and then 2 deg to the right. From then on, the fixation target remained centered in the visual field, and the subject's task was to attempt steady fixation of the target before, during, and following an eyeblink. To begin a trial, the subject began fixating and then pushed a button. Two seconds later a tone sounded to signal the start of the 3-sec interval during which the eye movement and EBG data could be collected. The subject attempted to make one bilateral blink of typical size during this period. A second tone sounded to signal the end of the data-collection period.

In order to change the orientation of the eye in the orbit, the bite bar was rotated 10 deg from the straight ahead position (as initially judged by the subject) in a clockwise, counter-clockwise, upward, or downward direction. Thus, the subject achieved a particular direction of gaze by fixating the target from the new position.

Motion Picture Records

Motion picture photography was used to sample the time course and amplitude of each subject's lid movements in executing a blink. Photographs were taken from nearly straight ahead, at speeds from 48 to 74 frames per second. Lid position data were taken from a small rectangular piece of thin tape placed on the lower margin of the upper lid. Frame-by-frame measurements of the horizontal and vertical edges of the tape could then be used to obtain precise records of motion of the lid during a blink.

The retraction of the eyeball was also measured photographically. For this purpose, the camera was placed to the side of the eye and somewhat below it. This oblique direction provided a side-on view of the lower portion of the cornea, thus permitting uninterrupted photography of the excursions of the eyeball and lids during blinks of moderate size.

Results

Moving Spot Observations

A spot of light that flies from left to right across the screen is typically seen as a horizontal streak that is

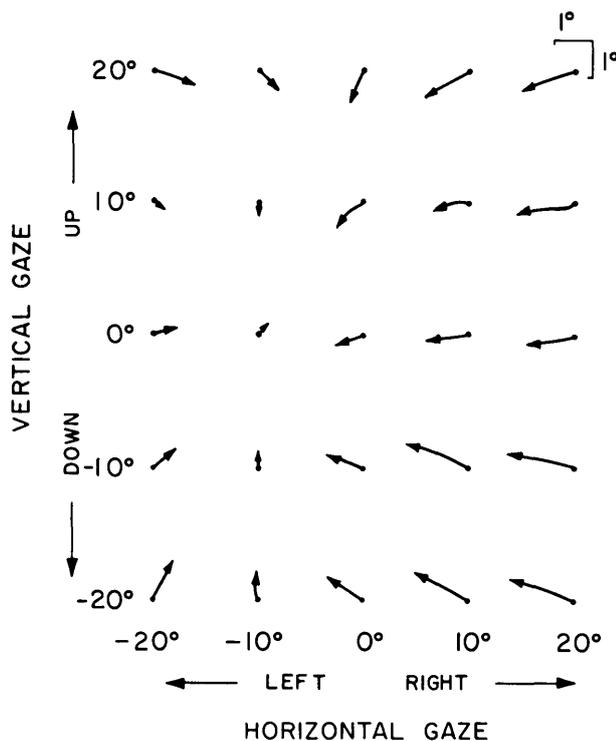


Fig. 6. Eye movement traces, with the stationary-spot method, showing effects of direction of gaze. Subject KAM, right eye, monocular viewing, showing amplitude and direction of eye movement prior to occlusion of vision by a normal voluntary blink.

momentarily deviated upwards at the time of a blink. This means that the eyes themselves have moved in the reverse direction, ie, downward, as shown in Figure 2 by the vertical deflections V_L and V_R . Similarly, a spot flying downwards is seen by the left eye to be deviated to the left, and by the right eye to the right, thus indicating horizontal deviations H_L and H_R of the two eyes, in the reversed (nasalward) direction, at the time of the blink. Note that a gap appears on each record. This means that the blink was extensive enough for the lids to close off the subject's view of the moving spot for the interval during which the upper lid has reached its lowest position. Note that in each case the eye has moved more rapidly than the lid, so that it has completed its downward and nasalward course and is on its way back to its resting position before the lid has produced the gap due to its own maximum closure.

Figure 3 contains sample eye movement tracings (E) for a more detailed comparison with records of upper lid closure (L). Points on L are from the separate frames of a motion picture film that shows the position of the lower margin of the upper lid. Records E and L are drawn with the same time scale, and the gap in E is made to coincide, as it should, with the lowest position of L. From this it is again clear that the eye movement follows a more rapid time course than the lid, especially

during the upward (return) phase of lid movement. In these records, the maximum velocity of lid closure is 181 mm/sec for LAR, and 309 mm/sec for JPK. This compares with a peak figure of 280 mm/sec cited by Collewijn et al for one of their subjects. The corresponding maximum velocities of eye movements are 46.5 deg/sec and 56.9 for these two subjects as compared to "about 75 deg/sec" cited by Collewijn et al¹⁰ for their subject.

Figure 4 presents sample records of the horizontal component of eye movements. These result from the right eye looking straight ahead (0 deg), and from 10 deg and 20 deg leftward gaze when the blink occurs. It is clear that the character of the eye movement changes, depending on direction of gaze. In general, as in this example, the eye movement at the time of a blink tends to be nasalward when looking straight ahead and in the direction of the primary position of the globe when other directions of gaze are adopted. Thus, during nasalward gaze the eye moves temporally, and vice versa. The horizontal and vertical components are well synchronized; in other words, the eye follows a nearly linear oblique trajectory.

Figure 5 presents an array of vertical eye movement traces derived from tracings by each of two subjects. It is clear that the predominant direction is downward; the amplitude of movement at the time of a blink increases when the subject is instructed to make increasingly strong blinks (going from top row to bottom). There is also some dependence of the amount of downward eye movement upon the vertical direction of gaze, but this is not nearly so marked a relationship in these vertical components as in the horizontal ones that appear in Figure 4. Note also that the wave forms of the traces in Figure 5 give added evidence of the relatively high speed of the eye movements, as illustrated in Figure 3. The downward motion of the eye typically starts gradually, but the major downward and subsequent upward movements of the eye, although not as rapid as saccades, are somewhat more rapid than is the case with the upper lid.

Stationary Spot Observations

Figures 6 and 7 contain arrays of eye movement records based on tracings of the apparent trajectory of a stationary bright spot at the time of a blink. Each arrow is a mirror image of the tracing made by the subject with monocular (right eye) fixation in the designated initial direction of horizontal and vertical gaze.

In Figure 6, each arrow shows the early portion of the eye movement that occurs when the lids execute a normal blink of medium strength. The dot indicates the starting position, and the tip of the arrow indicates the limiting extent of the eye movement that occurs

before vision is occluded by the upper lid. In most cases the arrow thus indicates the whole amplitude of the eye movement, as may be judged from the fact (see Fig. 5) that the eye is already on the way back to its original position before occlusion of the trace.

We may safely conclude from Figure 6 that the extent and direction of eye movement at the time of a blink are systematically related to the direction of gaze at the time that the eye movement starts. The data thus support a previous conclusion⁶ that a blink tends to move the eye in the direction of primary regard, and that a particular direction of gaze can be found near that of primary regard for which very little eye movement takes place. Nevertheless, recall that the "straight-ahead" (0 deg horizontal and 0 deg vertical) direction of gaze is defined only by the subject's judgment of direction. Subjects differ somewhat in the consistency with which the eye movement is determined by the direction of gaze. In general, too, we have found a stronger effect of eccentricity in horizontal gaze than in vertical.

When the upper lid is taped open, attempts to blink again produce eye movements toward the direction of primary regard. In fact, the results with upward gaze directions are similar to those shown in Figure 6 for the unrestrained lid condition. With downward gaze, however, the records (not shown) reveal abnormally large upward rotations of the eye when the upper lid is restrained.

Figure 7 shows the array of traces when both eyelids are taped open. The effect of lid taping is greatest for eye movements proceeding from the downward directions of gaze. Here the movement amplitudes are clearly larger than in the condition of Figure 6 (untaped lids). One must keep in mind, however, that taping the lids open is a procedure that is not well controlled. The amount of tension on each of the lids makes a considerable difference in the eye movements. Indeed, holding both lids open with the fingers can have the result that different degrees of upward or downward eye movement accompany the blink, depending on the relative tension exerted on the upper or lower lid. A subject can learn, with a little practice, to hold the lids open in such a way that the eye moves scarcely at all when a blink is attempted.

Eyeball Retraction

Motion picture records, made at a speed of 64 frames per second, show the closure of the lids and the simultaneous retraction of the eye during a voluntary blink. Frame-by-frame measurements are shown in Figure 8 for upper eyelid lowering and inward motion of the cornea in three subjects making small blinks and larger blinks. It is clear from these samples that the

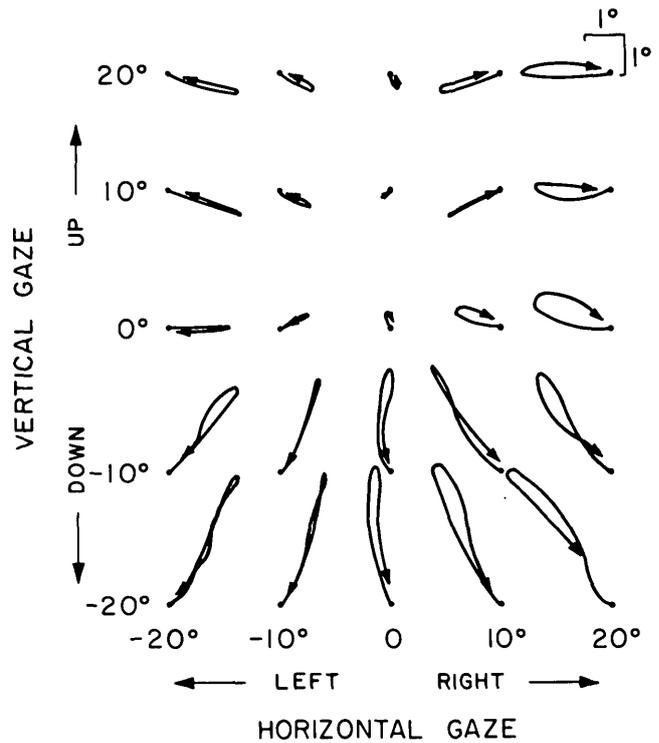


Fig. 7. Stationary-spot traces as in Figure 6 but with both upper and lower lids taped open. Subject KAM.

time course of retraction resembles that of the lid motion, and that less retraction occurs with small blinks than with large. Clearly the time course of retraction (in-and-out) is slower than the horizontal or vertical (rotary) motion of the eyeball that was illustrated in Figure 3.

Eyetracker Records

Use of the eyetracker is limited to conditions in which the pupil is not obstructed. Figures 9 and 10

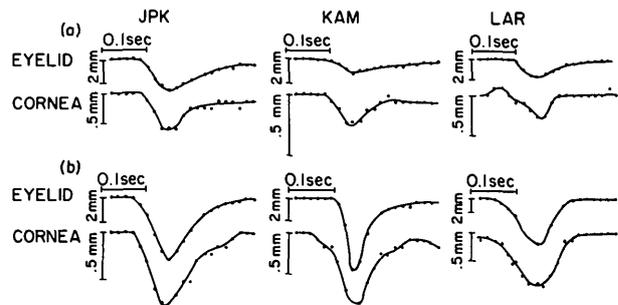


Fig. 8. Photographic measurements (64 frames/sec) of eyeball retraction during small blinks (upper) and larger blinks (lower). Size of blink indicated by amplitude of upper eyelid lowering. Eyeball retraction indicated by inward motion of the cornea. Measurements are based on film records showing an oblique view of the cornea and eyelids from below and to the side of the eye. The true excursions are thus slightly larger than indicated in this figure.

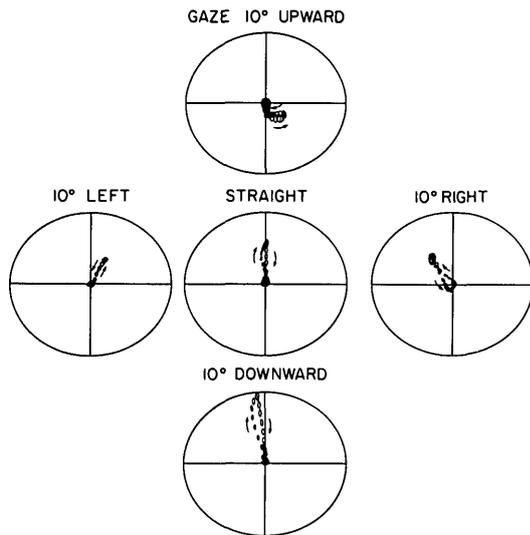


Fig. 9. Polar plots of moderate blinks. Effect of direction of gaze on movement of the eye at the time of a blink. Records made by eye tracker with both upper and lower lids taped open. Reference line at a radius of 3 deg. Subject KAM, right eye, monocular viewing. Compare with the visual persistence results in Figure 7.

contain records of right eye movements in a subject (KAM) who tolerated well the taping open of the lids. These are polar print-outs in which the center of the cross represents the straight-ahead position of the eye during fixation. Vertical eye movements are plotted above (upwards) and below (downwards) the center. Horizontal components are plotted toward the right (temporally) and left (medially) of the center. Each print-out contains a reference line that represents a 3-deg (Fig. 9) or 2-deg (Fig. 10) radial distance from center. The average position of the eye, sampled in ten successive records, is shown by the center of each small ellipse. The ellipse itself represents 0.1 standard deviation. The ellipses are drawn by the computer at 4-msec intervals. Thus, the distance between adjacent ellipses indicates the speed with which the eye movement occurred so that faster movements produced ellipses that are farther apart. Maximum velocity in this case is approximately 75 deg/sec, which is the same figure cited by Collewijn et al.¹⁰

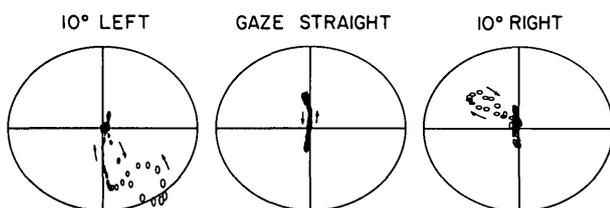


Fig. 10. Eye tracker records with upper lid taped open. Subject KAM, right eye, monocular viewing, small blinks, reference radius 2 deg.

When the records in Figure 9 were obtained, the upper and lower lids were both drawn away from the eye. When a blink was attempted during straight-ahead viewing, the eye moved smoothly upwards approximately 2 deg and looped downwards back to the position of initial fixation. During 10 deg leftward viewing, the eye moved obliquely upward and to the right as the blink was attempted. When viewing was 10 deg to the right, the blink attempt resulted in an oblique movement of the eye to the left and upward. With upward viewing there was a small movement down and to the right. The eye followed the same path to return to initial fixation at the end of the movement. With downward viewing, a large vertical movement, roughly 3 deg in extent, was accompanied by a slight horizontal component. Regardless of initial direction of regard, after each blink the eye returned very nearly to the point of fixation over a basically similar path.

The effects of a blink shown in the eye tracker records of Figure 9 may be compared with the visual persistence tracings made by the same subject in Figure 7. In both cases the lids were restrained by taping; and the downward, upward, left, and right directions of gaze resulted in blink-induced eye movements in the opposite directions. There is, however, some discrepancy that is probably due to a slight difference in the subject's choice of the primary (0 deg) gaze directions in the two experimental situations. Nevertheless, it is clear that the two methods are in agreement in demonstrating that eye movements accompany a blink even when both are retracted. Eyetracker records were also obtained from subject KAM when the upper lid, but not the lower, was taped away from the eye. These records (not shown) confirm those obtained from the same subject in the visual persistence observations. That is, taping the upper lid yields abnormally large upward eye movements when gaze is directed downwards.

Figure 10 presents the eyetracker results for eye movements taking place during blinks of small amplitude. These records, made with the upper lid taped open, confirm the previous observations: Smaller blinks are accompanied by small eye movements, and gaze to the right or left results in eye movements toward the direction of primary regard. Velocity of these smaller movements reaches a maximum of about 37 deg/sec.

Discussion

In attempting to understand our results, we turn to a consideration of the anatomy and physiology of muscles that are active during a blink.¹² The closing (downward) phase of upper lid movement is mainly due to activation of the orbicularis oculi. The opening (upward) phase results from activation of the levator palpebrae. These muscles are reciprocally driven; the

levator normally maintains sufficient tonus to hold the eye open, but relaxes during the rapid down phase caused by the orbicularis. The succeeding upward phase results from relaxation of the orbicularis and resumption of levator activity.

The retraction of the human eye during a blink is explained by Evinger et al.⁹ as due to a co-contraction of the external ocular muscles. This explanation, amply backed up by observations on laboratory animals and by some human EMG records, fits in with the anatomical fact¹² that "the rectus muscles arise from a common origin at the apex of the orbit." Normal saccades and other eye movements mainly involve rotation of the globe, a product of the reciprocal activity of opposite muscles. Little rotation would occur, however, if all muscles were equally and synchronously activated; instead, the muscle contractions would pull the globe back toward the apex of the orbit, ie, the retraction that accompanies a blink.⁹

With these considerations in mind, we may attempt to account for our own observations on eye movements that accompany a blink.

We agree with the conclusion of recent observers⁸⁻¹⁰ that there is no good evidence for any large, upward rotation of the eyes during a normal blink (Bell's phenomenon) as reported by Miles¹ and perpetuated in the clinical literature.⁵ The recent results, including our own, indicate instead that small, partly conjugate and partly disjunctive eye movements accompany a blink. Each eye rotates with an amplitude and in a direction that is strongly influenced by initial conditions of direction of gaze and lid position. The disjunctive nature and relatively slow velocity of the eye movements confirm the conclusion¹⁰ that they are not saccades.

The globe retracts into the orbit with a time course that parallels the closing and reopening of the lids. This finding might seem to suggest that the inward retraction of the globe is simply the result of a passive force exerted by lid closure upon the front of the eye. But, Evinger et al⁹ have found that retraction also occurs when the lids are held open during the attempt to blink. This finding leads to their conclusion that it is not the lids, but the extraocular muscles that apply the force for retraction.

We provide additional evidence for many of the findings of Evinger et al⁹ and Collewijn et al¹⁰ with regard to the time course of the eye movements that accompany a blink. Especially puzzling, however, is our own discovery that eye rotation has typically reached a maximum amplitude and started back again before the lids are fully closed. Thereafter, the lids reopen so slowly that the eye has rotated back to its initial position long before the complete reopening of the eye. We know that eye rotation normally involves a recip-

rocal activity of oppositely located rectus muscles. If we accept the co-contraction hypothesis for eye retraction, therefore, it may be necessary to modify it slightly in order to account for eye rotation. The modification could be of the sort that there is typically a slight initial imbalance among the rectus muscles, such that they co-contrast with slightly unequal force. The result would be what we observe: a retraction of the globe is accompanied by a small initial rotation. The imbalance could disappear as the globe becomes fully retracted, since at that point all recti would have reached full contraction. Thus, the initial rotation of the globe would be followed by the counter-rotation that we have observed. As the recti relax, and the globe moves forward to its normal position in the orbit, we observe that there is an early return of the eye to its initial direction of regard.

Starting with Ginsborg and Maurice⁶ several investigators have made the observation, most clearly shown in our Figure 6, that a blink causes the eye to rotate toward its primary position in the orbit. Evinger et al have pointed out that this would naturally be the case if we recognize the co-contraction of all the extraocular muscles. If the blink occurs, for example, when the eye is gazing downward, the inferior rectus is already partially active and will not participate as vigorously as the superior rectus and the other muscles in the co-contraction. Hence the eye will exhibit an upward rotation at the outset of the blink, an example of the strong dependency that we have observed between the extent and direction of eye movement and the direction of gaze.

Restraining the lids is shown (Fig. 7) to produce abnormally large eye movements under certain conditions. It is nevertheless true that with or without lid restraint a particular direction of gaze can be found for which little or no eye rotation takes place at the time of a blink. We interpret this to mean that the orbicularis, levator, and external ocular muscles are then in an equilibrium position with respect to the forces that each can exert upon the globe.

Finally, the fact that blinks involve such a complex interplay of orbicular and extra-ocular muscles prevents us from drawing any firm conclusions about whether the orbicular, as well as the extra-ocular muscle system may be associated with the visual suppression that is known to accompany a blink.¹¹ We have found no evidence that blinks are accompanied by any saccades or vergence movements that could account for the suppression.¹³⁻¹⁶ But a single efferent system activates the orbicularis and the recti to produce lid closure and eyeball retraction.¹² It would seem likely that suppression is a corollary of this efferent action at the time of a blink.

Key words: blinks, eye movements, visual persistence, eye tracker, lid movements

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