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Blinking and Associated Eye Movements in Humans, Guinea Pigs, and Rabbits

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SUMMARY AND CONCLUSIONS

1. Recordings of upper eyelid movements in humans, guinea pigs, and rabbits demonstrated that all three species displayed qualitatively similar patterns of eyelid movement. The relation between amplitude, duration, and maximum velocity in rabbits and humans was nearly identical. Guinea pig blinks were faster than those of rabbit and man.

2. Electromyographic (EMG) recordings in humans demonstrated that the orbicularis oculis muscle participated in downward movement of the upper eyelid during blinks and eyelid closure but did not participate actively in the downward lid movement occurring with gaze changes.

3. When looking straight ahead, the estimated stiffness and viscosity of the upper eyelid were 10 g/mm and 0.38 $g \cdot s \cdot mm^{-1}$ for humans and 1.17 g/mm and 0.062 $g \cdot s \cdot mm^{-1}$ for rabbits.

4. Upward and abducting rotations of the eye accompanied blinks in rabbits and guinea pigs. Simultaneously, the eyeball retracted (translational movement) into the orbit. These translational and rotational eye movements resulted from contraction of the retractor bulbi muscle and cocontraction of antagonistic extraocular muscles. The data suggested that humans also retracted the eye during voluntary blinks. The retraction produced a rotation of the eye toward a "primary position" rather than a rotation in one specific direction.

5. The relationship between the maximum velocity, duration, and amplitude of the down phase of a blink may be expressed as a single equation, maximum velocity = $c \times$ average velocity, where c is a constant. The same relationship, with a similar value for c, also describes saccadic eye movements and rapid skeletal movements. This implies that all three movements employ comparable neural mechanisms.

INTRODUCTION

In humans, the oculomotor system interacts constantly with blinking. Every blink produces a momentary suppression of vision (69) and is accompanied by an eye movement (5, 15, 25, 26, 50). To minimize the potentially disruptive effects of a blink on ongoing extraocular activity, the oculomotor system appears to regulate the occurrence of blinking. For example, smooth-pursuit eye movements result in an almost total suppression of spontaneous blinking (65; C. Evinger, unpublished observations). On the other hand, saccadic eye movements tend to be accompanied by blinks (72; C. Evinger unpublished observations), and blinks almost always accompany rapid combined eye and head movements (C. Evinger, unpublished observations). Thus, reciprocal actions occur between blinking and eye movements. Blinks cause a disruptive effect on extraocular activity by engendering an eye movement and suppressing vision. The oculomotor system regulates blinking by suppressing it at times when its effects would be most deleterious and initiating a blink at times when it would be least disruptive.

The present study begins an examination of the effects of blinking on the oculomotor system. In particular it focuses on the dynamics of blinking and the eye movements accompanying a blink. To provide a data base for subsequent studies on the anatomical and

physiological basis of the eye movement accompanying a blink, the present paper provides data on rabbits and guinea pigs as well as humans.

METHODS

This study employed three species: humans, rabbits, and guinea pigs. Three of the authors served as the human subjects; four pigmented rabbits, two albino rabbits (2–3 kg) and two pigmented guinea pigs (400–600 g) served as the other subjects. Eyelid position and velocity, eye position and velocity, and orbicularis oculis, superior rectus, and inferior rectus electromyograms (EMGs) were monitored. Eyelid movements were either spontaneous blinks or were elicited by gentle puffs of air to the periorbital region or by requesting the subject to blink, close the eyes, or change the direction of gaze.

Eyelid position recording

Several methods of measuring eyelid position were tried, but the best one proved to be a lever system. A lever attached to the lower margin of the upper eyelid by double-stick tape moved a small infrared light-emmitting diode past a photosensitive position detector (United Detector Technology, SC-50) fixed approximately 1 mm from the diode. The lever was constructed of thin-walled 1-mm-diameter glass tubing mounted on a fulcrum of two silk threads (5-0). The output of the photosensitive position detector was differentially amplified (Tektronix AM 502; DC–300 Hz, −3 dB), displayed on an oscilloscope, and stored on analog tape for later analysis by hand. Even after storage on the tape, the system easily resolved 200 μm of movement and possessed a band pass of 300 Hz without hysteresis. After every session, the output of the detector was calibrated by moving the lever along a ruler. Analog differentiation (100 Hz, −3 dB) of the detector output provided a measure of eyelid velocity.

The lever arrangement offered little resistance to lid movement. In support of this, high-speed photographic analysis of human eyelid movements produced results very similar to those obtained with the present system (13, 33). Likewise, the lever did not appear to impede the lid movements of the guinea pigs. Although the smallest animals in the study, they achieved higher lid velocities than humans or rabbits. Thus, the lid position monitor provided an accurate reflection of lid motion.

Eye position recording

In guinea pigs and rabbits, eye movements were monitored with the scleral search-coil technique (54; DC–1,000 Hz, −3 dB). Under general anesthesia (xylazine, acepromazine, ketamine; Ref. 59), eye coils were implanted according to the method of Judge et al. (35). In addition, a dental acrylic crown was created for head restraint. After several days of recovery, testing began with the animals fully alert. Eye position was calibrated by rotating the driving coils around the animals through a known angle. Since neither guinea pigs nor rabbits exhibited many spontaneous eye movements during head restraint, this method gave very reliable and consistent calibrations.

EMG recording

In humans, EMGs were recorded by means of two electrodes taped to the temporal and nasal aspects of the upper lid. The electrodes were two chloride-coated silver plates (2 mm diameter) coated with a small amount of electrode paste to reduce their impedance. The small size of the electrodes meant that the EMG could be recorded simultaneously with the eyelid movement. The EMG signals were amplified differentially (10–3,000 Hz, −3 dB), full-wave rectified, and then "integrated" with a low-pass analog filter.

In two rabbits, EMG electrodes were implanted in the superior and inferior rectus muscles of the left eye. Under general anesthesia (59), two Teflon-coated multistranded stainless steel wires (0.002 inch bare; 0.009 inch coated), bared approximately 1 mm, were implanted, one into the belly of the superior rectus muscle and the other into the belly of the inferior rectus. A third electrode, a flattened silver wire, was placed on the skull to serve as a ground. A dental acrylic crown was created for head restraint and the two EMG leads and ground wire were secured to this platform. After several days of recovery, testing began with the rabbits fully alert. Treatment of the EMG signal was identical with that described above.

Application of weights to eyelid

In order to estimate the stiffness and viscosity of the upper eyelid, a weight was applied suddenly to the lid and the resultant displacement and the maximum velocity achieved during the displacement were measured with the lid monitor. To apply weights, a silk suture (4-0) was attached to the eyelid with double-stick tape near the attachment of the lid monitor. The suture ran through a double pulley system so that the suture pulled nearly straight down on the eyelid but the weight (Ohaus standard weight) tied to the suture hung away from the face. This allowed unimpeded movement of the weight. For each trial the investigator held the suture so that there was no slack but also so no weight was applied to the lid. This could be checked by observing the output of the lid monitor. If tension on the string was too high, adding slack to the string produced an upward movement of the lid. When the tension was correct, adding slack to the suture did not result in a change in lid position. At unpredictable intevals, the investigator released the string, thereby applying the weight to the eyelid. After the lid achieved its final position, the investigator lifted the weight rap-

idly, which produced considerable slack in the suture. Figure 1*C* shows a typical trial in a human. Since the apparatus registered a 10-fold difference in the stiffness of rabbit and human eyelids, the mechanical characteristics of the system probably played a minimal role in the results.

All data including velocity records were stored on a Hewlett-Packard eight-channel tape recorder. For analysis, the data were written out on an ultraviolet light-beam recorder at speeds of 25 cm/s. All data analyses were performed by hand. The duration of a lid movement was defined as the time between when the lid first began to move till when the velocity first returned to zero.

Photography

The translational eye movements accompanying eyelid closure in human subjects were recorded photographically. After taping the left eyelid open away from the eye and securing the head by means of chin and forehead rest bars, photographs of the profile of the left eye were taken from the left side when the subject had both eyes open and while the subject attempted to close his eyes. The photographs were taken with a Cannon AE-1 35-mm single-lens reflex camera equipped with a macrolens capable of 1 to 1 reproduction. Each picture included a ruler fixed in front of the left eye in order to superimpose different photographs.

RESULTS

Dynamics of lid movement with blinking

Photographs of blinking showed that the motions of the eyelids exhibited some species differences. In humans the upper eyelid traversed a downward and medial trajectory, while in rabbits and guinea pigs the upper eyelid path was downward and lateral. Although this report deals exclusively with upper eyelid movements, it is worthwhile noting that in humans the lower lid moved primarily medially, while in rabbits and guinea pigs it moved primarily upward, with a small medial component.

Despite differences in trajectory, the dynamics of the upper lid movements during a blink were similar in all three species (Fig. 1).

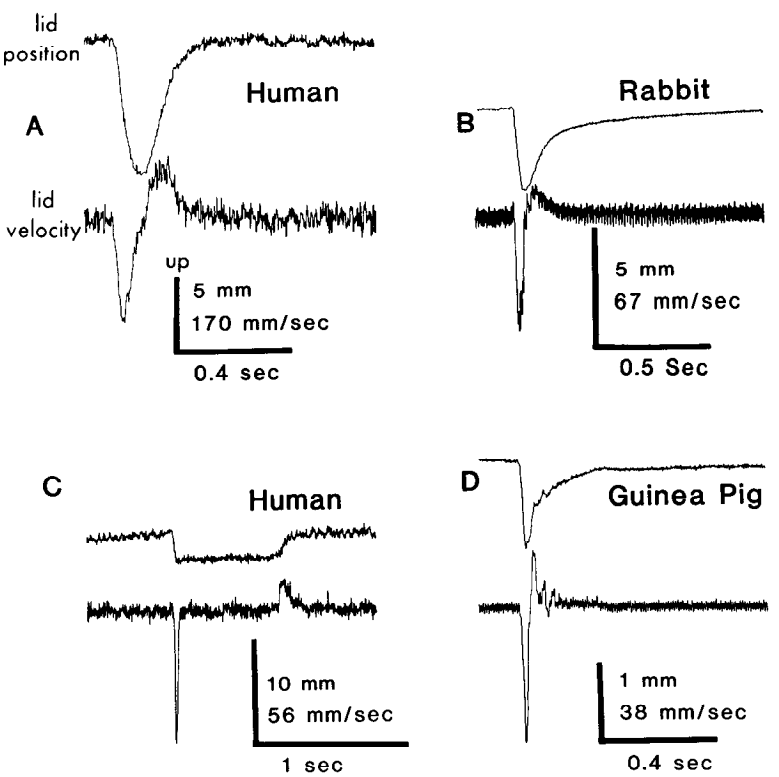

FIG. 1. Vertical movements of the upper eyelid during blinking and mechanical displacement. *A, B, D*: individual records of lid position and velocity during a blink in three species. *C*: individual record of human lid position and velocity produced by suddenly applying a weight to the upper lid (downward deflection) and then removing it (upward deflection) when the eye was looking 40° down. Downward deflections represent downward movements of the lid.

The down phase (closing the eyelid) exhibited shorter durations and achieved higher velocities than the up phase (opening the eyelid). The down phase occurred as a single, smooth movement. In contrast, the up phase displayed two stages: an initial rapid rise, followed by a slower exponential-like approach to the final lid position. Guinea pigs and rabbits most clearly demonstrated these separate stages.

Quantitative analysis of lid dynamics demonstrated that the metrics of human blinks were similar to those of rabbits but were slower than those of guinea pigs (Fig. 2). For example, a 2-mm lid movement in the human (down phase) required 86 (±47 (SD) ms; $n = 11$) and achieved a maximum velocity of 44.1 ± 10 mm/s ($n = 11$). For the rabbit, the same movement required 89 ± 18 ms ($n = 23$) and achieved a maximum velocity of 43.9 ± 12 mm/s ($n = 23$). For the guinea pig, however, the duration was slightly less than half as long, 41 ± 16 ms ($n = 13$) and the maximum velocity was greater than twice as fast, 94.9 ± 15 mm/s ($n = 13$). The same species ranking held for the maximum velocity of the up phase but not for the duration. A 2-mm lid movement achieved a maximum velocity of 21.5 ± 18 mm/s ($n = 15$) in the human, 16.8 ± 6 mm/s ($n = 20$) in the rabbit, and 39.3 ± 17 mm/s ($n = 6$) in the guinea pig. Nevertheless, the

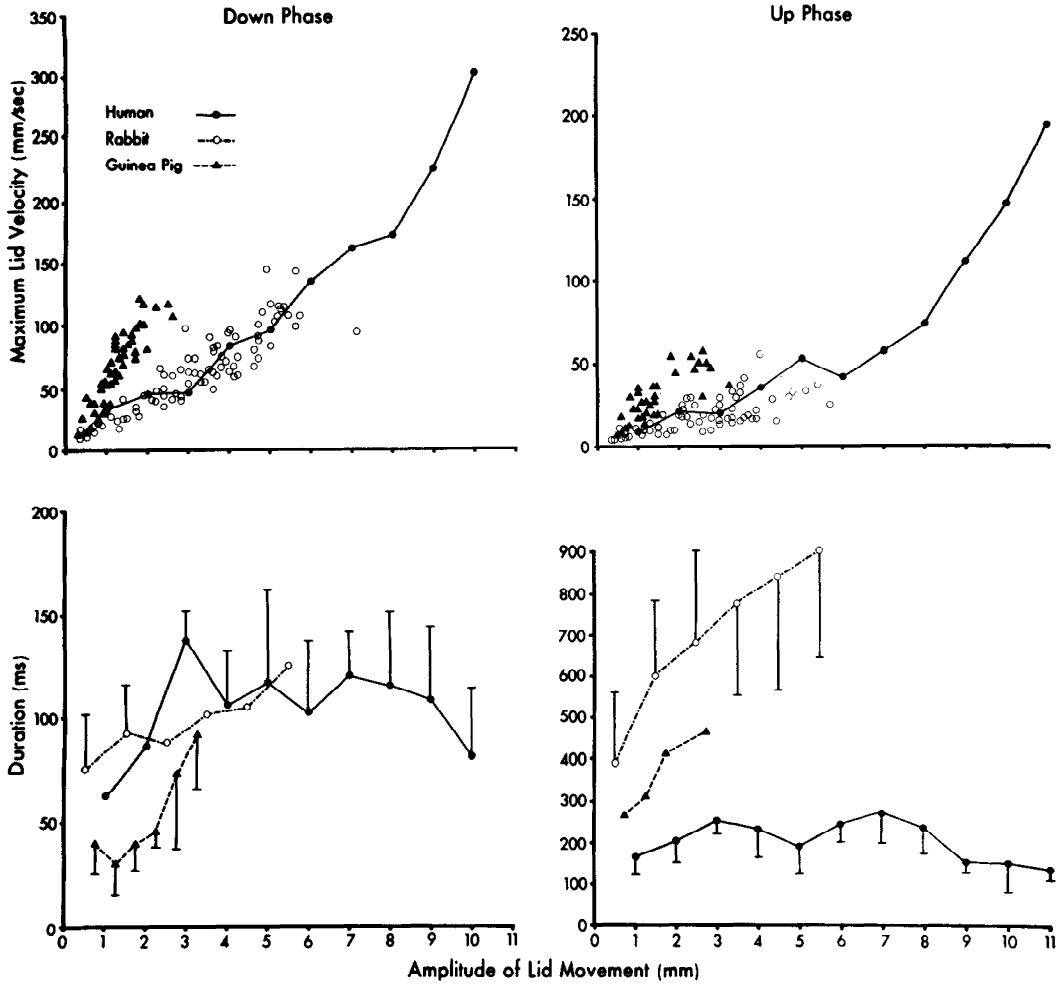

FIG. 2. Maximum velocity and duration of the upper eyelid movement as a function of blink amplitude for downward and upward movements of the lid for a human, a rabbit, and a guinea pig. Each point represents a single blink. The connected points represent the mean of at least 10 blinks. Error bars indicate 1 SD.

durations of the movement were 200 ± 50 ms (n = 15) for the human, 652 ± 207 ms (n = 20) for the rabbit, and 382 ± 119 ms (n = 6) for the guinea pig. The slow exponential-like stage of the up phase (Fig. 1) accounted for the discrepancy between the maximum velocity and duration results. The second stage was slower in rabbits and guinea pigs than in humans, resulting in longer overall durations despite the high maximum velocities attained in the initial portion of the up phase. An additional subject from each species yielded results quantitatively similar to those shown in Fig. 2. The results for humans matched very closely the data from other investigators on the metrics of human blinks (13, 27, 33, 41).

The human data confirmed previous observations made on large-amplitude lid movements (33). At large amplitudes, the duration of the down phase decreased rather than increased (Fig. 2). Concomitant with the decreased duration, maximum velocity increased. Such large-amplitude movements occurred only when subjects were instructed to blink or "flutter" the eyelids. Spontaneous blinks rarely exceeded 6 mm in amplitude

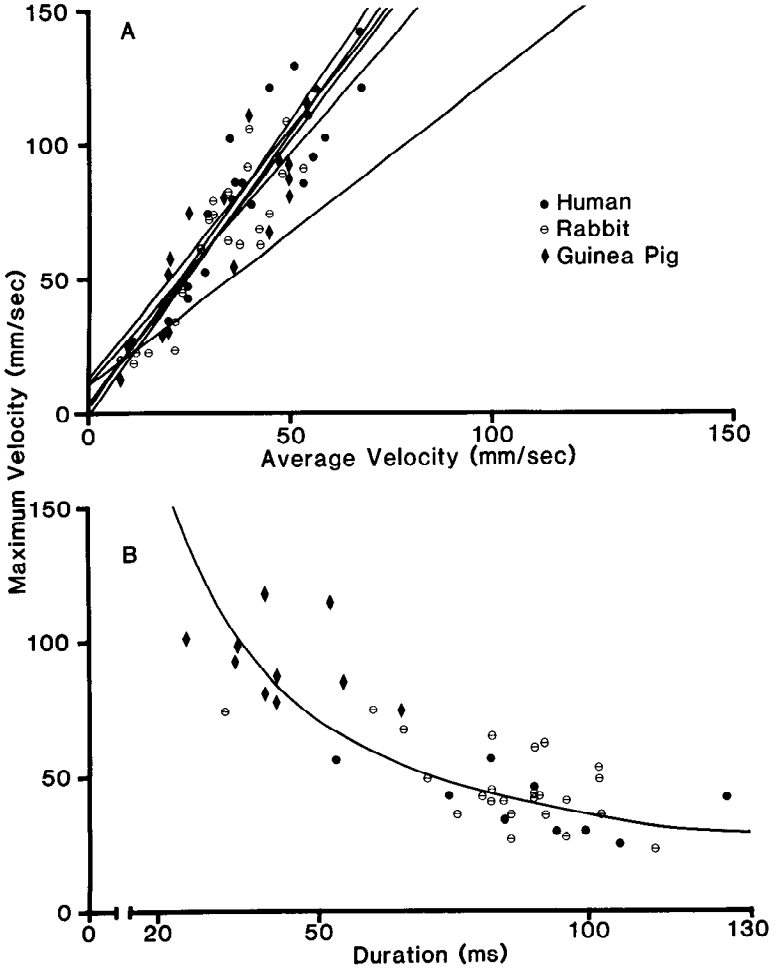

FIG. 3. *A*: linear regression lines of maximum lid velocity as a function of average lid velocity for the down phase of a blink in humans, rabbits, and guinea pigs. Each symbol represents a single observation. For clarity only some of the values are plotted. Each regression line was calculated from at least 50 points. *B*: maximum downward lid velocity of 2-mm blinks (1.5- to 2.5-mm bin) as a function of lid duration for humans, rabbits, and guinea pigs. Each symbol represents a single observation. The solid line was derived from *equation 4* using c = 1.77 (mean of all six animals).

(13, 41). The poor correlation between duration and amplitude suggested that the metrics of the lid movements were more typical of skeletal ballistic movements than of saccadic eye movements (22).

In the down phase of a blink, maximum velocity is linearly proportional to average velocity (Fig. 3*A*). The correlation coefficients range from 0.82 to 0.94 and each regression calculation used at least 50 points. From this relation it follows that

$$V_m = m1 \text{ amplitude} + b1 \quad (1)$$

$$V_a = m2 \text{ amplitude} + b2 \quad (2)$$

where V_m is maximum velocity, V_a is average velocity, and m and b are constants. Rearranging *equation 2*

$$\text{amplitude} = (V_a - b2)/m2$$

Substituting for amplitude in *equation 1*

$$V_m = m1((V_a - b2)/m2) + b1$$

$$V_m = (m1/m2)\, V_a - (m1/m2)\, b2 + b1 \quad (3)$$

Since $m1/m2$ scales $b2$ to equal $b1$, the last two terms can be dropped. Then

$$V_m = (m1/m2)Va \quad \text{let } c = m1/m2$$

$$V_m = c\,(\text{amplitude/duration}) \quad (4)$$

$$\text{amplitude} = (V_m \times \text{duration})/c \quad (5)$$

Thus, for any given amplitude, the relationship between duration and maximum velocity must be constant, yielding a hyperbolic function when maximum velocity is plotted against duration (Fig. 3*B*). Moreover, the equation shows that neither maximum velocity nor duration alone is sufficient to describe the down phase of a blink. The value of c (slope of the maximum velocity-average velocity relationship; Fig. 3*A*) for the down phase of the blink, ranged from 1.13 to 2.17 (mean = 1.77 ± 0.37; n = 6) with the values being idiosyncratic for individuals rather than for different species. Since the value of c is very similar for all species despite differences in amplitude-duration-maximum velocity relationships, the data for all animals at any given amplitude is well fitted by a single hyperbolic curve with c = 1.77 (Fig. 3*A*). This same set of equations with similar values for c may also be applied to saccadic eye movements and ballistic skeletal movements (see DISCUSSION).

Role of orbicularis oculis and levator palpebrae muscles in saccadic gaze changes and blinking

The orbicularis oculis muscle always participated in blinking but did not actively contribute to the lid movements accompanying downward saccadic eye movements (Fig. 4).

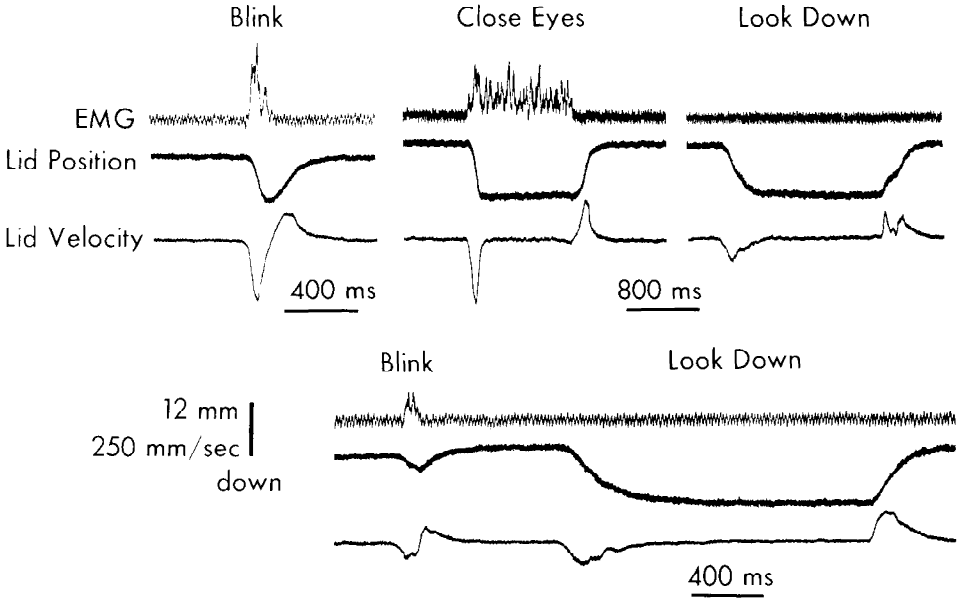

FIG. 4. Human orbicularis oculis EMG activity associated with blinking, closing the eyes, and looking down. The EMG activity was rectified and low-pass filtered.

Closing the eyes and holding them closed resulted from sustained orbicularis oculis activity, but lid movements of nearly equal amplitude generated by looking down that did not completely close the palpebral fissure engendered no EMG activity. It is possible that the EMG activity associated with low-velocity movements failed to rise above the noise level. This explanation is unlikely, however, because EMG activity accompanied small-amplitude, low-velocity blinks but not higher velocity lid movements produced by large downward saccadic eye movements (Fig. 4). Thus orbicularis oculis activity associated with blinks is different from that associated with saccadic gaze changes. Earlier investigators using needle EMG electrodes also concluded that orbicularis oculis activation did not occur with lid movements accompanying gaze changes (7, 15, 27, 67). The reader can convince himself of this result by putting a finger on the lateral canthus, just at the edge of the eyelid, and

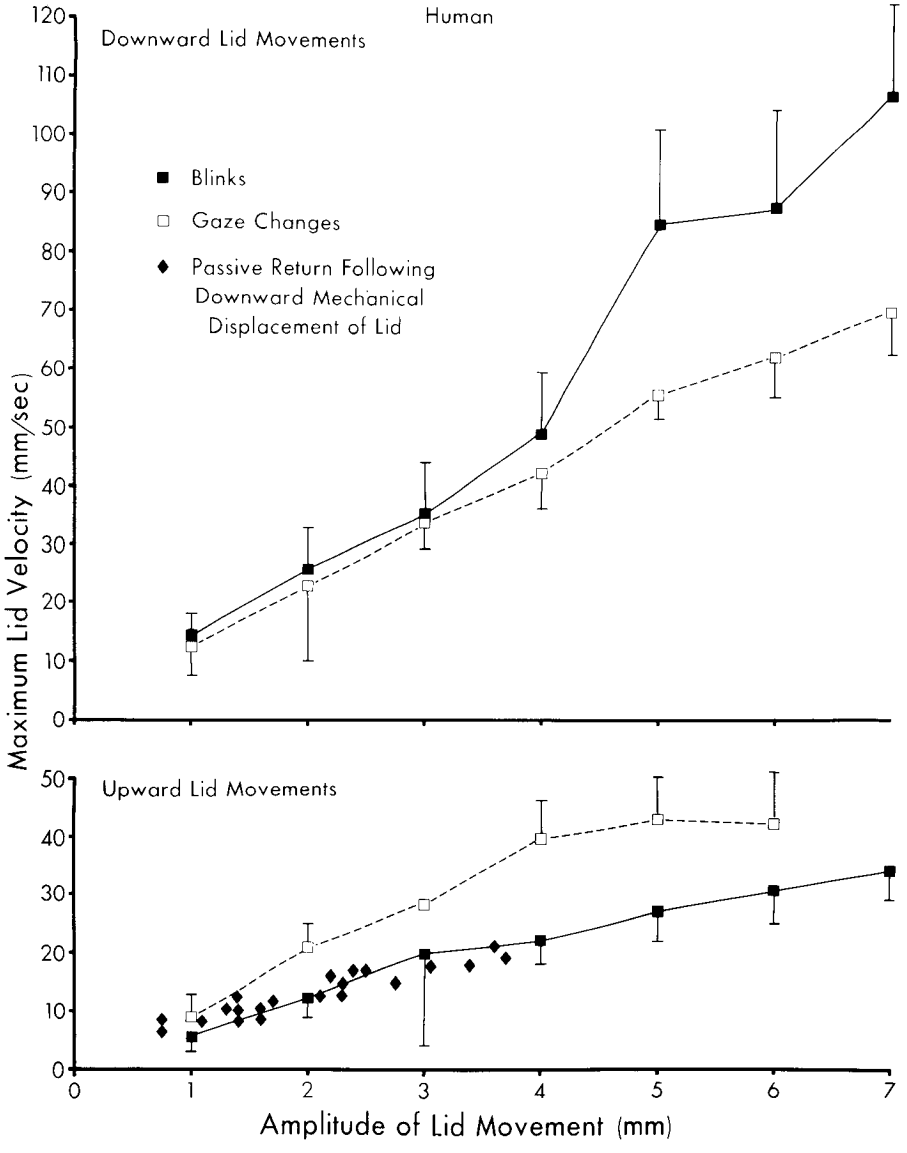

FIG. 5. Lid velocity as a function of the amplitude of lid movement for blinks (filled square) and saccadic gaze changes (open square). Each point is the mean of at least 10 observations and the error bars indicate 1 SD. The standard errors of the mean are smaller than symbols. The diamond symbols show the maximum velocity of the passive return of the lid following mechanical displacement of the lid. Each diamond represents an individual trial.

blinking. A strong tug from contraction of the orbicularis oculis can be felt. However, looking up and down so that large lid excursions occur fails to produce such a tug. Since the orbicularis oculis is the only muscle producing palpebral closure, the lid movement accompanying downward saccadic eye movements must result from a passive downward tension on the upper eyelid. As the tonic activity of the levator palpebrae muscle decreases, a concomitant reduction of its upward tension on the eyelid occurs. The eyelid then descends until the passive downward tension equals the decreased upward tension generated by the levator palpebrae muscle. Consistent with this interpretation, the maximum lid velocity of the down phase of a blink (active contraction of the orbicularis oculis; Fig. 4) always exceeded the maximum velocity of the downward eyelid movement accompanying a downward saccadic eye movement (Fig. 5). Thus, changes in the levator palpebrae activity control lid movements during saccadic gaze changes.

EMG studies demonstrate that the activity of the levator palpebrae ceases during a blink, but is similar to that of the superior rectus at all other times (15). This suggests that lid movement during the up phase of a blink will differ from the movement accompanying an upward saccadic eye movement. Following the cessation of levator palpebrae activity accompanying a blink, the levator resumes the same level of activity it exhibited prior to the blink. This is equivalent to applying a "step" of activity to the levator palpebrae muscle. During an upward saccadic eye movement, however, the levator muscle probably receives an input like that to the superior rectus, a "pulse-step." This latter input should produce a faster upward eyelid movement than that accompanying a blink. Figure 5 supports this interpretation. Likewise, if this description is correct, the upward lid movement during a blink should be identical to that produced by mechanically displacing the lid downward and then releasing it. This was tested by suddenly applying and then removing a weight hung on the upper eyelid and monitoring the movement of the lid (Fig. 1*C*). The maximum lid velocity of the eyelid following release from mechanical displacement matched the maximum velocity attained by the lid during the up phase of a blink (Fig. 5). Likewise, the shape of the velocity profile following release from mechanical displacement was similar to

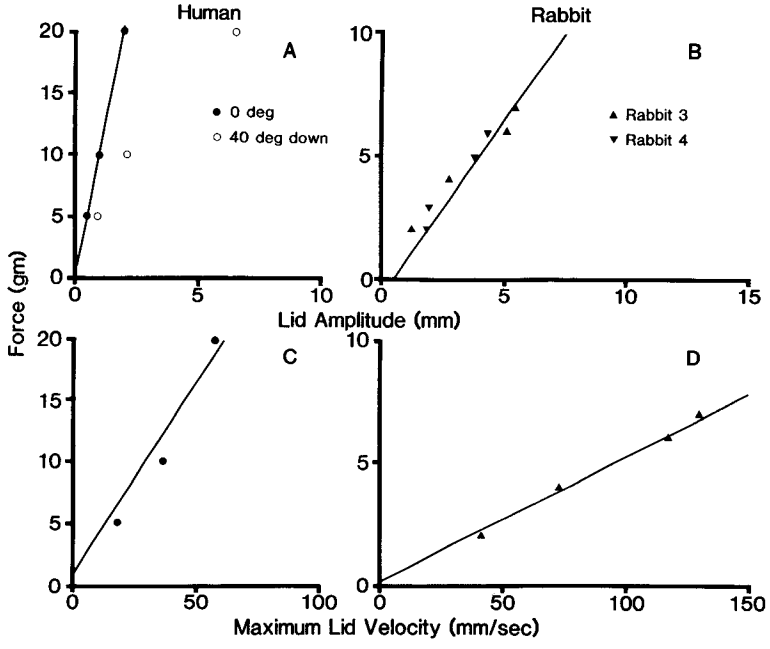

FIG. 6. Mean downward displacement and maximum velocity of the upper lid caused by hanging different sized weights on the lid in a human (*CE*) and two rabbits. Each point is the mean of at least five observations.

that of the upward phase of a blink (Fig. 1*A*, *C*). These results support the conclusion that a step input into the levator palpebrae muscle produces the upward phase of a blink.

Stiffness and viscosity of upper eyelid

Measurements of the amplitude and velocity of downward lid displacement, produced by hanging weights on the upper lid (Fig. 1*C*), yielded estimates of upper lid (primarily levator palpebrae muscle) stiffness and viscosity (Fig. 6). These values depended upon the direction of gaze. The upper lid stiffness of a human looking 40° downward was 2.5 g/mm, but when looking straight ahead (primary position) stiffness increased to 10 g/mm (Fig. 6*A*). With the eye in the primary position, the rabbit upper lid exhibited considerably less stiffness than the human (1.17 g/mm; Fig. 6*B*). Similarly, other rabbit extraocular muscles offer less stiffness than human extraocular muscles (3). The viscosity of the rabbit upper lid was also less than that of humans looking straight ahead (0.55 g/(mm/s); Fig. 6*D* versus 0.38 g/(mm/s); Fig. 6*C*). Therefore, it was not surprising that following removal of the weight, the passive return of the lid took longer for rabbits than for humans. The predicted human time constant (0.38 g/(mm/s)/10 g/mm = 0.038 s), however, was somewhat less than the measured time constant 0.062 s). The predicted time constant for the rabbit (0.055 g/(mm/s)/1.17 g/mm = 0.047 s) fell far short of the observed time constant (0.25 s).

Eye movements accompanying blinks

Ever since 1823 when Bell (5) reported an upward rotation of the eyes during a blink (Bell's sign), it has been known that an eye movement accompanies human blinks. Later investigations, however, provided conflicting accounts as to the size and even the direction of the eye movement. Little data are available on the presence or absence of Bell's sign in nonhuman species.

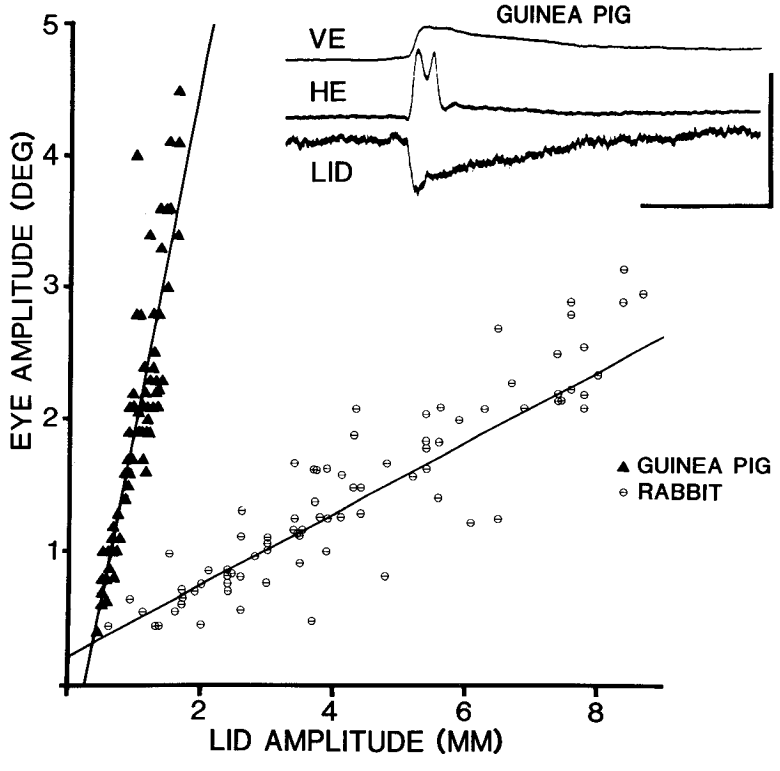

FIG. 7. Eye movements associated with blinking. The graph shows the amplitude of the vertical component of the eye movement accompanying a blink as a function of blink amplitude. The inset is an individual record of a guinea pig's eye movements during a blink. Upward deflections represent upward rotations for the vertical component (VE) and abducting rotations for the horizontal component (HE) and upward movements of the lid. The calibration lines represent 10°, 3.3 mm, and 500 ms.

Guinea pigs and rabbits exhibited an upward and abducting eye rotation during a blink. In rabbits both the horizontal and vertical components of the eye rotation were very stereotyped (Fig. 8). Guinea pigs, however, exhibited considerable variability in the amplitude and shape of the horizontal component (Fig. 7, inset). The vertical movement, therefore, was used to compare the two species. The relationship between blink amplitude and the amplitude of the vertical component of the eye movement differed between the two species (Fig. 7). For guinea pigs, the slope of this regression line was 2.7°/mm (n = 67; r = 0.86) and for rabbits the slope was 0.28°/mm (n = 83; r = 0.90). The maximum velocity of the eye movements accompanying blinks was in a range similar to saccadic eye movements.

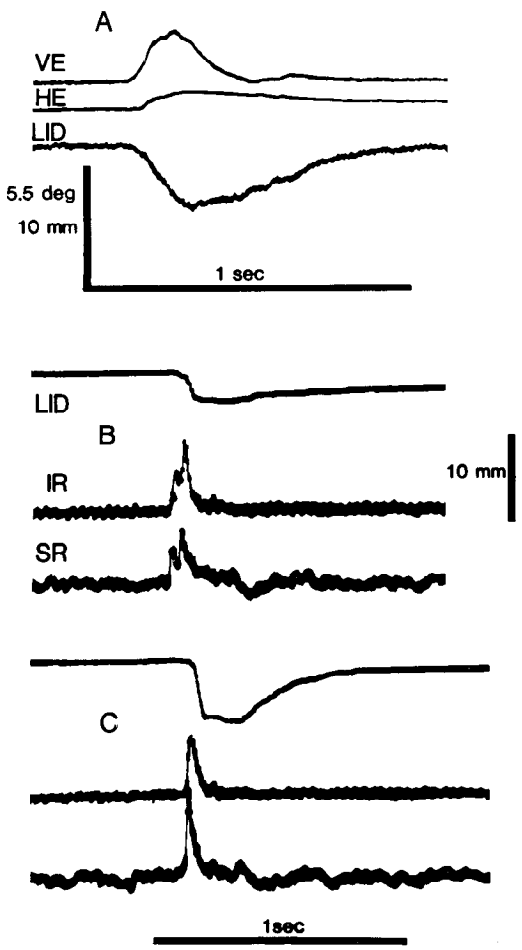

FIG. 8. Rabbit eye movements (A) and extraocular EMG activity (B, C) associated with a blink. HE and VE are the horizontal and vertical components of the eye movement. The EMG activity of the left inferior rectus (IR) and left superior rectus (SR) muscles during two blinks are shown. EMG records were rectified and low-pass filtered.

The eye movements accompanying the blinks of guinea pigs and rabbits may not be rotations produced by patterned inputs to the extraocular muscles. Rather, the eye rotation may be the secondary effect of retracting the eyeball into the orbit, a movement to which the eye-coil system is insensitive. Two arguments support this idea. First, both the guinea pig and the rabbit possess retractor bulbi muscles (16, 52), which are known to pull the eye back in the orbit during a blink. Second, the complicated rotational trajectory of the guinea pig eye during a blink is explained more parsimoniously by assuming it is secondary to eye retraction rather than assuming the elaborate pattern of inputs to extraocular motoneurons necessary to produce such eye rotations. Nevertheless, the rotational trajectory of the rabbit eye during a blink is consistent with activation of the superior rectus muscle (29, 61), as has been reported in human blinking (15). To test this hypothesis, EMG activity in one eye was recorded simultaneously from the rabbit superior rectus and its anatagonist, the inferior rectus. Both muscles showed a vigorous burst of activity during a blink (Fig. 8) but exhibited the expected anatagonistic activity during slow rotations about the roll ("barbecue spit") axis. Since both the inferior rectus and superior rectus contract during a blink, the typical Bell's sign seen on blinking in the rabbit appears to be a secondary action of eyeball retraction.

Although humans do not have a retractor bulbi system (64), cocontraction of the extraocular muscles during a blink could produce globe retraction. The reader can demonstrate movement of the eye back into the orbit during a blink by very gently placing a finger on the closed eyelid over the pupil of one eye and closing the eyes or blinking. The eyeball will be felt to move rapidly back into the orbit. In two subjects this retraction was measured by attaching a low-torque potentiometer via a light-weight arm to the closed upper lid over the pupil so that the potentiometer could only register anterior-posterior movements. In the other eye, the usual lid monitor measured the up and down movements of the lid. These

measurements showed an inward movement of the globe of 1.5 mm (maximal excursion) with dynamics similar to those of the up and down movements of the lid (Fig. 9). One possible explanation for these results, however, was that the contraction of the orbicularis oculis mechanically forced the eye back into the orbit. To eliminate this factor, photographs of the eye were taken with the lid taped open, drawing the lid away from the globe. The subject was asked to blink or close both eyes (Fig. 9). The photographs showed quite clearly the eye movement back into the orbit. The change in pupil position relative to the bridge of the nose before and during attempted lid closure demonstrated the retraction. Both subjects exhibited similar retraction. Figure 9 also shows tracings of the two photographs that were superimposed, using the ruler included in the photographs (not shown) as the point of reference. The filled pupil is with the eye open, the dotted line shows the pupil position during attempted eye closure. In addition to retraction, the eye exhibited a small upward rotation. The direction of eye rotation, however, was not identical for every trial. In some cases the eyeball rotated down and in other cases to the left or right. The direction of rotation seemed to depend on the position of the eye in the orbit preceding the blink. The reader can demonstrate this dependence on eye position for himself by fixating a dim light in a dark room and blinking. (These conditions minimize the effects of backward masking (10).) When looking straight ahead, blinking produces only a small image motion of the light. After turning the head to the left while fixating the light so as to rotate the eyes far to the right, blinking causes a rapid rightward image motion. After tilting the head down while fixating the light so as to rotate the eyes far up, blinking creates a rapid upward image motion of the light. Similarly, blinking after turning the head to the right or tilting it

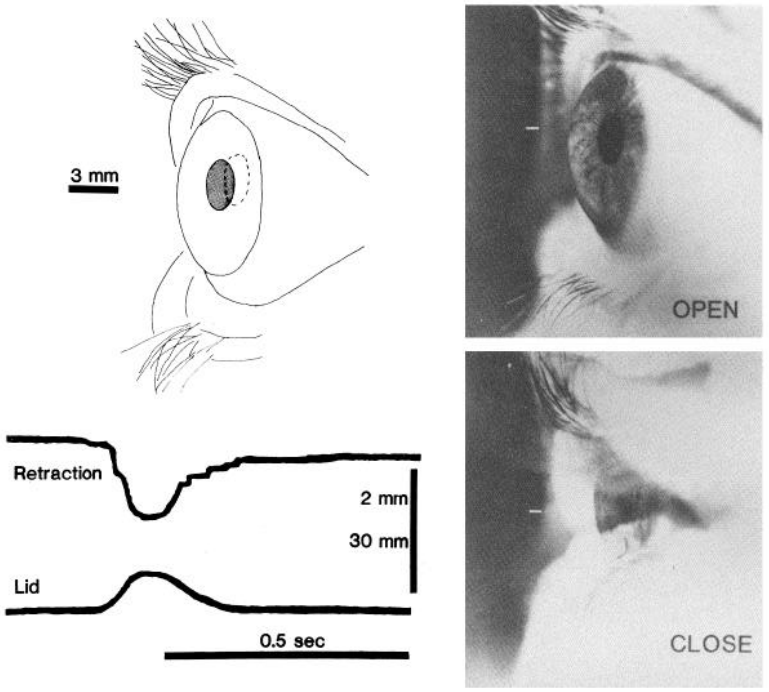

FIG. 9. Movements of the human eye during eyelid closure. Photographs show the left eye in profile with both eyes open (open) and when instructed to close eyes (close). Tape attached to margins of eyelids held the left eyelid open and away from the globe. The eye retraction may be seen by comparing the distance from the pupil to the bridge of the nose (bar) in the two pictures. Superimposed tracings of the two pictures also show the retraction. The shaded pupil is the eye-open condition; the dotted pupil is the eye-closed condition. The individual record demonstrates dynamics of the eye retraction during a blink. The method is described in the text. The 2-mm calibration refers to the retraction trace.

upward produces an image motion of the light to the left or down, respectively. Such image motion is explained by eyeball rotation in a direction opposite the direction the eye is looking. Therefore, the eyeball rotation in the examples just presented shows that the eye rotates back toward the center of the orbit during a blink. In a similar paradigm, Ginsborg and Maurice (26) obtained identical results. While the possibility exists that the extraocular muscles receive different patterns of activity during a blink depending on the location of the eye in the orbit, it seems more likely that cocontraction of several or all of the extraocular muscles retracts the eyeball into the orbit, secondarily rotating the eye toward some primary position.

DISCUSSION

Role of orbicularis oculi and levator palpebrae muscles in blinking and saccadic gaze changes

In blinking, the orbicularis oculis plays an active role and the levator palpebrae performs a primarily passive role. Prior to the blink, the tonically discharging levator ceases discharging and the orbicularis oculis produces a burst of activity, pulling the lid down. When the orbicularis oculis ceases discharging, the levator palpebrae resumes its previous tonic activity and the upper lid returns to its initial position (7, 15, 27, 67). The down phase is produced by a short burst of activity above the normal level, which may conveniently be described as a pulse, similar to the signal that generates saccadic eye movements. The up phase is produced by a sudden change in the tonic level of activity, which may be described as a step, similar to the signal that generates vergence eye movements (39). It is not surprising, therefore, that the up and down phases of a blink display very different dynamic properties. The down phase of a blink achieves higher maximum velocities than the up phase (Figs. 1, 2, 5; Refs. 13, 27, 33, 41) and occurs as a single smooth movement. In contrast, the up phase consists of two stages, a rapid rise followed by a slower, exponential-like approach to the final lid position (Fig. 1). Thus, the down phase behaves like a typical rapid movement, e.g., a saccade, while the up phase is dynamically similar to a vergence movement. Consistent with the idea of a step increase in neural activity producing the up phase, the maximum velocity of the passive return of the eyelid following downward mechanical displacement matches the velocity of the up phase of blinking (Fig. 5). Thus, the neural inputs appear to dictate the dynamics of the up and down phases while the difference in mechanical properties between rabbit and human eyelids determines the differences in the metrics of the up phases (Figs. 1 and 6).

In lid movements associated with gaze changes, the levator palpebrae plays an active role and the orbicularis oculis performs primarily a passive role. This paper (Fig. 4) and earlier studies (7, 15, 27, 67) document the absence of any change in orbicularis oculis activity during saccadic gaze changes. Other studies also document the modulation of levator palpebrae activity with gaze changes (7, 15, 27, 67). Since the orbicularis oculis is the only muscle producing downward lid movement, a constant, passive downward tension must exist on the upper eyelid such that relaxation of the levator palpebrae results in downward movement of the lid. Gravity alone cannot account for this downward force since normal lid movements accompany saccades when subjects stand on their heads (58). The force probably arises from the mechanical properties of the eyelid system. Kennard and Smyth (42) reached a similar conclusion from biomechanical experiments. When looking down, the levator palpebrae relaxes and the upper lid moves downward until the passive downward force on it matches the decreased upward force of the levator palpebrae. This interpretation explains the common clinical observation that lesions of the facial nerve result in abnormal lid movements during attempted eye closure but normal lid movements with saccadic eye movements. The lid movements accompanying upward gaze changes probably occur because the levator palpebrae muscle receives a pulse-step input. Given that the levator palpebrae motoneurons are in the oculomotor nucleus and that oculomotor motoneurons exhibit a pulse-step discharge pattern for saccadic eye movements, the levator palpebrae motoneurons would be expected to show a similar discharge profile. Consistent with this interpretation, during upward saccades the eyelid achieves higher maximum velocities than during the up phase of a blink (Fig. 5).

With this organization, the facial nucleus need not obtain eye-position information in order to alter eyelid position with gaze changes. Interestingly, in cats and rabbits the facial nucleus does receive such information via collaterals from vestibular nucleus neurons that carry eye-position and head-velocity signals to extraocular motoneurons (28, 49, 60). These inputs are inhibitory and do not exert a detectable effect on orbicularis oculis motoneuron activity in the present paradigm. The vestibular input, however, may play a role in the suppression of spontaneous blinking accompanying smooth-pursuit eye movements. Nevertheless, it seems reasonable to conclude that the eye movement signals carried by the levator palpebrae motoneurons alone are sufficient to ensure coordinated lid and eye movements during saccadic gaze changes.

Stiffness and viscosity of upper eyelid

While no stiffness or viscosity values for the rabbit eyelid existed prior to this study, comparable human data are available. With the subject looking 45° down, Hung et al. (33) estimated a lid stiffness of 1.5 g/mm and a viscosity of 0.09 g/(mm/s). With a slightly more elevated gaze (40° down), the present experiments found a stiffness of 2.5 g/mm and a viscosity of 0.2 g/(mm/s). Since lowering the gaze reduced stiffness and viscosity, these results are comparable.

Barmack (3) provided stiffness measurements of rabbit and human extraocular muscles. Rabbits exhibited a stiffness of 0.11 g/deg. Assuming an 18-mm eyeball diameter (52) this value converts to 0.7 g/mm, a somewhat lower value than the 1.17 g/mm found in the present study (Fig. 6). The ratio of human extraocular stiffness (1.09 g/deg) to rabbit extraocular muscle stiffness (0.11 g/deg) is 0.1. This is nearly identical to the ratios for human and rabbit eyelid stiffness. In the present study, the ratio of human to rabbit eyelid stiffness when in the primary position is 0.12 [(1.17 g/mm)/(10 g/mm)]. Thus, the present results are consistent with other measures of extraocular muscle stiffness.

For both humans and rabbits the time constant predicted from the stiffness and viscosity measurements underestimated the observed time constant. This suggests the presence of a second viscoelastic element in the lid that produces the much slower "creep" toward final position. Human extraocular muscles exhibit a similar second viscoelastic element (12). Since the up phase of a blink is equivalent to releasing a weight from the eyelid, the presence of a second viscoelastic element would explain the two stages of the up phase of a blink (Fig. 1).

Eye movements accompanying blinks

It is clinically accepted that an upward rotation of the eye accompanies blinking in humans. Surprisingly, however, experimental studies have yielded quite disparate results. Using photographic techniques, Miles (50) reported that the eye moved upward and nasalward 10–15° during the down phase of a blink. Using nearly identical procedures, Ginsborg (25) reported an upward and nasalward eye movement, but found it to be less than 100′ of arc. Electrooculographic (EOG) measurements suggested upward rotations of up to 60° (66); however, EOG measurements during a blink probably do not reflect the actual movement of the eye (4, 56). Recent studies in humans using the eye-coil system found a slight downward rotation of the eye with blinking (H. Collewijn, personal communication). Using a psychophysical technique as in the present paper, Ginsborg and Maurice (26) reported that rather than rotating in one specific direction during a blink, the eye rotated to a primary position in the orbit. Such a pattern of eye movement during blinking might explain much of the disparity between the results reported by other authors.

Since cocontraction of antagonistic pairs of muscles would cause an apparent rotation of the eye to a primary position in the orbit, eye retraction in humans offers a physiological mechanism for Ginsborg and Maurice's (26) result. The present paper demonstrates eye retraction in humans during eye closure with the eyelid held open (Fig. 9). Previous authors have also noted the occurrence of human eye retraction during blinking with the eyelid closed (13) and with it open (51, 55). Since humans do not have a retractor bulbi muscle (64), eye retraction must result from cocontraction of the extraocular muscles. Consistent with this interpretation, EMG studies demonstrate that at least the lateral (8) and superior rectus (15) muscles exhibit a burst of activity with reflex blinking.

At first glance it seems unusual to conclude

that the human eye retracts during a blink and that cocontraction of the extraocular muscles produces the retraction. However, since extraocular muscle cocontraction is found throughout the vertebrate line, it would be more surprising if humans did not exhibit eye retraction. For example, fish, which do not have a retractor bulbi muscle, exhibit a strong eye retraction reflex to corneal or orbital stimulation (70). The existence of trigeminal inputs to oculomotor motoneurons (44) may account for the eye retraction. On the other hand, eye retraction produced by contraction of the retractor bulbi muscle is typically associated with the presence of a movable nictitating membrane. It is not surprising, therefore, that with a reflex blink, a rabbit exhibits cocontraction of the extraocular muscles, as well as contraction of the retractor bulbi muscle (Fig. 8; Refs. 6, 47). Similarly, birds also exhibit cocontraction of the extraocular muscles during a blink (C. Evinger, unpublished observations) although retraction of the eye has no effect on the nictitating membrane (70). Thus cocontraction of extraocular muscles is probably a basic, protective, eye reflex.

The existence of cocontraction in human extraocular muscles during blinking may help to explain some clinical observations. In the syndrome of retraction nystagmus, damage to the midbrain periaqueductal region causes a retractory nystagmus generated by cocontraction of extraocular muscles (24). Attempted up gaze or vertical optokinetic nystagmus (fast phase up) initiates this nystagmus. This syndrome can be explained by assuming that up gaze pathologically releases the normal eye retraction associated with blinking. In contrast, alternate explanations must assume the generation of a whole new pattern of input to motoneurons, a much less parsimonious explanation of this syndrome. Cocontraction of extraocular muscles during a blink may also help to explain why some patients with Huntington's disease (45) or posterior fossa abnormalities (72) can only make normal-velocity saccades in association with a blink. For cocontraction during a blink to occur, all the extraocular motoneurons must receive an excitatory input. In contrast, for a saccade to occur, the agonist motoneurons must receive an excitatory input and the anatagonist motoneurons must be inhibited. If the excitatory saccadic input in these patients is abnormally weak, saccadic eye movements will be unusually slow. If the patient initiates a saccade and a blink simultaneously, however, the blink excitation of the agonist motoneuron will facilitate the saccadic excitation, but the blink excitation of the anatagonist motoneuron will be lost in the normal saccadic inhibition. This could produce a near-normal saccade.

Single description of rapid lid, eye, and arm movements

The down phase of a blink is an excellent example of a rapid movement. Its dynamics, particularly in humans, are similar to rapid skeletal movements (22) in that movement amplitude correlates poorly with movement duration (Fig. 2). In contrast, the amplitude of saccadic eye movements correlates very well with movement duration (2, 17, 23, 30). Nevertheless, this distinction between skeletal and extraocular rapid movements may be misleading. In all those cases, ballistic skeletal movements, saccadic eye movements, and the down phase of a blink, maximum velocity is linearly porportional to average velocity (18, 21, 22, 57; Fig. 3*A*). This means that movement amplitude is proportional to maximum velocity, duration, and a constant, c (*equation 4*). Two implications of this result are apparent.

First, the equation suggests one reason why investigators have postulated different control systems for skeletal and saccadic movements. For any given amplitude, the relationship between duration and maximum velocity must be constant, yielding a hyperbolic function when maximum velocity is plotted as a function of duration (Fig. 3*B*). Ballistic skeletal movements operate at low velocities and long durations. At a given amplitude, duration can vary widely with only small changes in maximum velocity on a hyperbolic curve such as Fig. 3*B*. Thus, in terms of the ease and accuracy of measurement, maximum velocity will be a much better predictor of movement amplitude. In contrast, saccadic eye movements operate at high velocities and short durations. For any given amplitude, maximum velocity can vary widely with only small changes in duration so that duration will be an easier measure of saccade amplitude.

Second, neither maximum velocity nor duration alone is sufficient to describe a rapid movement. At least two of the three values (amplitude, maximum velocity, and duration) are required. Experiments on oblique saccades

and two-handed movements confirm this conclusion. Oblique saccades may be viewed as a combination of a horizontal and a vertical saccade. Horizontal and vertical saccades use different extraocular muscle pairs and are organized in different brain stem areas (see Refs. 1, 23 for review). If the horizontal and vertical components of oblique saccades retain this independence, then the amplitude-duration-maximum velocity relationships dictate that components of unequal size will have different durations and maximum velocities. For example, the horizontal component of a cat oblique saccade directed 10° down and 4° left should finish 25 ms before the vertical component. In fact, the duration of the smaller component of the oblique saccade is increased until it is almost equal to that of the larger component. Concomitantly, the maximum velocity of the shorter component decreases (17, 18, 30). Neither a duration nor a maximum velocity code adequately explains this result. Kelso et al. (40) designed an experiment for two-handed movements conceptually similar to the oblique saccade experiments. From Fitts' law (19, 20), the movement time to a target depends on the log of movement amplitude to movement precision (target size). For example, the duration of a 24-cm movement to a 7.3-cm target is 3.7 times longer than a 6-cm movement to the same target. Kelso et al. (40) required subjects to move both hands simultaneously to targets that differed in expected movement time. If the movements were independent, one hand should reach its target before the other. Instead the hands reached the targets simultaneously. This occurred because the velocity of the hand movement to the easier target was slowed. These experiments demonstrate that neither duration nor maximum velocity by itself offers an accurate code for the amplitude of a rapid skeletal or saccadic eye movement because the values vary according to the movement condition. *Equation 4* incorporates all three relevant variables and provides an accurate description of these movements regardless of the conditions.

Quantitative analysis of the discharge of burst neurons in the reticular formation involved in generating saccadic eye movements suggests a possible strategy for neural control of rapid movements. Three significant relationships exist between saccade and burst neuron discharge characteristics. First, saccade duration correlates with burst duration. Second, maximum velocity correlates with average burst frequency (9, 14, 31, 32, 34, 36–38, 43, 48, 62, 63, 68). Third, saccade amplitude correlates with the number of spikes in a burst (31, 36–38, 43, 71). For each saccade amplitude, the burst neuron emits a constant number of spikes regardless of saccade duration or maximum velocity. This corresponds well with the relation between maximum velocity and duration (Fig. 3*A*). Replacing maximum velocity by average firing frequency and saccade duration by burst duration produces a hyperbolic curve of a constant numbers of spikes (average firing frequency (spikes/s $\times$ burst duration (s) = constant number of spikes), just as amplitude does in Fig. 3*B*. In this way the number of spikes would determine amplitude and how the spikes were delivered would determine maximum velocity and duration. Lestienne (46) obtained a similar hyperbolic relationship between EMG duration and integrated EMG amplitude for constant-amplitude arm movements.

Interestingly, the value of c (the slope of the maximum velocity-average velocity relationship) is strikingly similar for different types of movements and species. Evinger et al. (18) reported that the value of c was 1.9 for saccadic eye movements for all mammalian species. Similarly, the value of c calculated from Freund and Budingen's (22) paper on isometric forearm contractions was 1.87. For the down phase of the blink, the mean value of c was 1.77. The fact that one equation can describe rapid movements of oculomotor, skeletal, and lid systems implies that all three employ comparable neural mechanisms.

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