Different forms of blinks and their two-stage control

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Summary. The purpose of this paper is to examine blink kinematics and the neural basis of blinks evoked reflexively by different kinds of stimuli. The kinematics of the upper lid movement and the electromyographic response of lid muscles levator palpebrae and orbicularis oculi were recorded in the rabbit during trigeminally and visually-evoked blinks. We find that there is a basic, kinematic difference between blinks. A blink in response to an airpuff is more rapidly accomplished and achieves a higher velocity than does an equal amplitude blink in response to a flash of light. The two forms of the reflex blink result from differences in the nature and timing of activity in antagonistic lid muscle motoneurons. Nevertheless, most characteristics of blink neural control are common to both reflex blinks. Most importantly, it appears that blinks are produced by two-stage neural control, an early component that is preprogrammed and a late component that is under stimulus control.

Key words: Blink – Trigeminal – Orbicularis oculi – Levator palpebrae – Eye lid

Introduction

The eyeblink is recognized as an important neural assay of brainstem integrity. Many recent studies have examined related aspects of blinking: eye movement during blinks (Collewijn et al. 1985; Evinger et al. 1984), vision during blinks (Manning et al. 1983; Riggs et al. 1981), and tearing (Doane 1980). Blinks have served as a model behavior for simple forms of learning: associative learning (McCormick and Thompson 1984; Yeo et al. 1985), reflex modification (Hoffman and Ison 1980; Uhlich et al. 1983), and adaptive plasticity (Evinger and Manning 1985). In spite of the recent interest in eyeblinks, some of their fundamental properties are not well understood.

An assumption underlying most studies is that a blink is a unitary movement and that once elicited, all blinks are alike. Nevertheless, many afferent pathways can evoke a blink and blink latency depends on the nature of the eliciting stimulus (Hopf et al. 1973; Kugelberg 1952; Rushworth 1962; Yates and Brown 1981; Zanetkin et al. 1979). Previous studies did not critically examine blink kinematics or the neural basis of blinks evoked by different stimuli, although Doane (1980) noted some differences in lid velocity between voluntary and spontaneous blinks in human subjects.

Although all blinks depend on the same lid muscles, the lid movements need not all be identical. For example, distinctly different forms of basic movements (e.g., postural adjustment) occur because of shifts in the timing of contractions in a set of muscles (for review see Nasher and McCollum 1985). The present study demonstrates that trigeminally- and visually-evoked blinks in the rabbit are kinematically distinct and this results from differences in the nature and timing of muscle contraction.

Moreover, our data suggest that treating an individual blink as a unitary movement obscures an important aspect of how the nervous system organizes blinks, and movement in general. For example, other simple movements such as smooth pursuit eye movements are actually comprised of two components, a short latency component that initiates the movement and a longer latency component that tailors the response to the characteristics of the stimulus (Liszberger and Westbrook 1985). The present study suggests that neural control of the blink reflex operates in a similar, two-part fashion. In both types of reflex blink, the initial blink lid movement is preprogrammed while the later component of the blink is under stimulus control.
Material and methods

Surgical procedure

The subjects of this experiment were six adult New Zealand albino rabbits (2 to 3.5 kg). Under general anesthesia (ketamine, acepromazine, xylazine; see Shaw and Alley, 1982) and sterile conditions, pairs of electrodes were imbedded in the lid muscles of four rabbits to serve as electromyographic (EMG) recording electrodes. The primary muscles involved in a blink are the orbicularis oculi (OO), a sphincter that encircles the eye and closes the eyelids, and the levator palpebrae (LP), which lies superior to the superior rectus muscle and inserts into the upper lid raising the upper lid. The EMG electrodes were placed centrally into the OO of the upper eyelid, a few mm from the lid margin, and into the LP, near the belly of the muscle. The end of each Teflon-coated, single-stranded stainless steel wire (0.003 inch bare; 0.0045 inch coated) was bared 1 mm, inserted into a 27 guage hypodermic needle, hooked at the needle tip and then the needle was slid into the muscle and withdrawn, leaving behind the implanted electrode wire. A silver wire that lay along the skull served as a ground electrode. The chronic, stimulating, nerve cuff containing two EMG-type wires was constructed from Teflon tubing (ID = 0.034", OD = 0.04") and implanted in two rabbits around the supraorbital branch of the trigeminal nerve, which was previously cleared of surrounding tissue. The EMG, ground, and nerve cuff wires passed under the skin towards the top of the head and connected to plugs in a dental acrylic crown that was secured to the skull with six screws. The crown attached to a fixed bar in the recording apparatus to restrain the head during data collection. Rabbits were given analgesic agents postoperatively to minimize discomfort. Rabbits first participated in experiments about 1 week after surgery, well after complete recovery. There was no indication that these procedures affected normal blinking in any manner.

Eyelid position

During experiments, a position-sensitive lid monitor was affixed to the upper eyelid to measure position of the eyelid in the vertical plane. One end of a counterbalanced, light-weight lever was attached to a silk thread secured to the lid near the center of the upper eyelid margin (Evinger et al. 1984). As the lid rose and fell, a light-emitting diode on the opposite end of the lever moved past a photosensitive position detector (United Detector Technology, SC-50). The output of the position detector was differentially amplified (Tektronix AM502; bandpass with -3 dB points at DC and 1 KHz). Analog differentiation (100 Hz, -3 dB) of the detector output provided a measure of eyelid velocity. The system was calibrated after every session by moving the lever through known distances. Since rabbits exhibit few spontaneous eye movements or blinks, neither lid position records or electromyographic records were subject to contamination due to unwanted eye movements.

Blink-evoking stimuli

The experiments were designed to elicit reflex blinks through visual or trigeminal afferent pathways. All rabbits blinked to flashes of bright light from a halogen lamp (American Optical). Light traveled through a fiber optic bundle and was aimed at the eye with a lens to illuminate an area approximately 2.5 cm in diameter. Lumiance, measured with a Tektronix J16 photometer with J623 probe, was varied from 350 to 21950 foot-Lamberts. A fast-acting electronic shutter (Uniblitz) interposed in the light path controlled flash duration from 25 to 500 ms. Light stimulus duration was confirmed with a photocell. Even after hundreds of trials, shutter activation by itself did not elicit a blink.

All rabbits also blinked in response to discrete puffs of air directed at the eye and periorbital region. Compressed air was channeled through rubber tubing to the narrow opening in a plastic pipette (5 mm long, <1 mm diameter at tip) 30 mm from the eye. Air pressure at the source was varied from 4 to 17 lbs/sq in. An electronically operated solenoid (General Valve) controlled duration of the airpuff, which ranged from 25 to 500 ms. To monitor stimulus onset and duration, a stretch of tubing identical to that going to the eye and sharing the same pressure source was directed towards a microphone 30 mm distant. The sounds of the airpuff alone did not elicit a blink. With rare exception, each air and light stimulus evoked only a single blink.

Finally, blinks were elicited by constant voltage pulses passed through the supraorbital nerve cuff in implanted rabbits. Blink-evoking pulses lasted 100 μs and voltage ranged from 20 to 50 V (WPI Digitimer and stimulus isolation unit). Voltage was slowly increased from 0 V until a blink occurred. Stimulation never exceeded 1.5 × threshold and rabbits never exhibited signs of discomfort.

Data collection

Alert, quiet rabbits were tested in 1 to ½ h sessions in which either stimulus duration or stimulus amplitude varied. Within each
session a full range of stimuli was presented in pseudo-randomly
ordered blocks of 9 to 12 trials. Blocks of airpuff trials alternated
with blocks of light flash trials. The computer controlled time
between trials which varied randomly from 12 to 18 s. The blink
response showed little habituation with this intertrial interval.
Repeating the first air and light conditions at the end of the session
provided an estimate of the variability in the data over the course
of testing. There was little or no difference between EMG or lid
data collected at the beginning and end of an experiment. Some
rabbits were used more than once in the same experiment or
participated in both amplitude and duration experiments. Rabbits
1 and 6 were tested with a more limited range of stimuli than were
the other animals.

Care for the rabbits' comfort was important since discomfort
or annoyance would result in unreliable responses and in the rabbit
closing his eyes, which would have ended the experiment.

Data analysis

Lid movement and EMG data from each trial were stored on
analog magnetic tape (8 channel Vetter instrumentation recorder)
for later off-line analysis. EMG responses were filtered (bandpass
with -3 dB points at 100 Hz and 3 kHz). Data were stored and
analyzed on an IBM PC (A/D conversion with 12 bit precision,
1000 Hz/channel for position and velocity and 6000 Hz/channel for
EMG). The computer displayed each blink record and picked the
beginning, the maximum excursion, and the maximum velocity of
the downward lid movement, although the user could amend these
values if necessary. For trials with EMG records, the computer
calculated the integral of the rectified and filtered (τ = 6.5 ms
EMG activity. The resulting blink data were analyzed individually
or averaged, omitting the first blink in each condition to eliminate
any startle effects.

Results

Differences between light- and air-evoked blinks

Rabbit blinks in response to trigeminal stimulation have shorter latencies than blinks in response to visual stimulation (air, 25 to 30 ms; light, 80 to
100 ms) as previously reported for other species (cat: Hiraoka and Shimamura 1977; Lindquist and Martenson 1970; rat: Hall and Hicks 1973; human:
Ongerboer de Visser 1980; Ongerboer de Visser et al. 1977; Rushworth 1962; Shahani and Young 1973). However, closer examination reveals a previously
unreported kinematic distinction between blinks elicited with trigeminal and visual stimuli.

During lid lowering with blinks of equal amplitude, the upper lid attains substantially greater velocity and acceleration in response to an airpuff
than to a light flash (Fig. 1). The velocity trace demonstrates that an air-evoked blink achieves a considerably greater downward lid velocity than does
an equal amplitude light-evoked blink. This kinematic difference extends across blinks of all amplitudes. This is clearly seen in plots of blink duration, the time
from the start of the lid movement until the lid achieves its maximum downward excursion, and
maximum lid velocity, the peak velocity achieved
during lid closure, as a function of blink amplitude,
the maximum excursion of the lid during the blink
(Fig. 2). The values of slope and y-intercept for best fitting straight lines fit to the data differ across
rabbits, but the basic pattern of results holds true for
all (Table 1). For the duration versus amplitude
relation, the mean y-intercept for light is approximately 1.5 times greater than that for air and the
slope for light is approximately three times as great as
that for air (which on average is just greater than 0).
The y-intercepts were not significantly different for
every rabbit (e.g., Fig. 2A), but the difference in
slope held for every animal (compare the magnitude
of the slope standard deviation to the Y-intercept
standard deviation in Table 1). Thus, light-evoked
blinks last longer for even small blinks, and as blink
amplitude increases, the duration of light-evoked
blinks increases more rapidly than does the duration
of air-evoked blinks. The duration of light-evoked
blinks is more varied, but nearly always exceeds the
duration of equal-amplitude air-evoked blinks.

For the velocity versus amplitude relation
(Fig. 2B), the y-intercepts for both light and air are
Table 1. Regression summary – rabbits 1 to 6

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<th>Duration vs amplitude relation</th>
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<td>Slope y-intercept (ms/mm)</td>
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Regressions are based on 200 blinks per rabbit on average. The median is probably the better measure of central tendency since n is small and some values are skewed.

similar, typically just greater than 0, but the slope for air is approximately twice as great as the slope for light. Thus, in both conditions lid velocity increases linearly with blink amplitude, but maximum lid velocity increases at a faster rate for air-evoked blinks. Because of the variability in values of slope and y-intercept across rabbits, the distinction between air and light functions is most striking for within rabbit comparisons. Nevertheless, after combining the data from all rabbits (Table 1), the light-air distinction remains clear.

Differences in muscle activity

The dissimilar kinematics of light- and air-elicited blinks must result from differences in lid muscle activity. In the upper lid, contraction of the levator palpebrae muscle (LP) raises the lid while contraction of the orbicularis oculi muscle (OO) plus a passive downward tension lowers the lid (see Evinger et al. 1984 for review). A blink occurs when the reciprocally acting muscles work in concert so that the LP relaxes and the OO contracts, producing the blink down phase, and then OO activity ceases and LP activity resumes, producing the blink up phase. This basic pattern of activity is present in both light- and air-evoked blinks. However, examination of EMG records reveals critical differences in EMG activity in the opposing lid muscles early in the blink.

First, OO activity differs between blinks. The EMOO exhibits a brisk burst of activity in response to an airpuff (Fig. 3A, unrectified records). In contrast, a light stimulus evokes a more gradual increase in EMOO and a more regular firing pattern. The differences in frequency of EMOO bursts in response to the air and light must affect the velocity of the resulting lid movement.

Second, there is a difference in the timing of activity in reciprocally acting lid muscles between blinks. In response to an airpuff, EMLP is quiescent by the time the initial burst of EMOO occurs (Fig. 3B, rectified records). Hence, the initial contraction of the OO occurs virtually unopposed by the LP. In contrast, in response to a light flash, the decrease in EMLP has scarcely begun when the burst in EMOO occurs. Therefore, the initial contraction of the OO must be opposed by the action of the LP. Moreover, LP records frequently show a slight increase in activity from baseline just prior to the light-evoked blink-related decrease in activity that is not evident during air-evoked blinks, which means the LP opposes even more the activity of the OO. Cocontraction of opposing lid muscles should reduce downward lid velocity relative to that found when the action of lid lowering muscles is unopposed. Thus, the difference in timing of activity in reciprocally-acting lid muscles, which is present across blinks of all amplitudes, contributes to the kinematic difference between light- and air-evoked blinks.

The difference between blinks may be modality dependent, rather than simply stimulus dependent. Electrical stimulation of the trigeminal supraorbital nerve also evokes blinks using the trigeminal pathway. The relatively weak stimuli elicit small blinks with EMOO burst characteristics typical of blinks evoked with supraorbital stimulation (Hiraoka and Shimamura 1977; Kugelberg 1952; Rushworth 1962; Shahani 1970). The latency of the earliest EMOO response is approximately 7 ms from stimulation. Electrical stimulation of the trigeminal supraorbital nerve produces the same temporal pattern of OO and LP activity found with airpuff-evoked blinks (Fig. 3C, unrectified records). The LP ceases discharging before the onset of the OO burst and resumes activity after completion of the OO activity. Plots of maximum downward lid velocity and blink duration as a function of blink amplitude yield a similar relation for blinks in response to supraorbital stimulation or to airpuffs. The weak amplitude shock intensity used here produced blinks no larger than 0.5 mm, so it is only possible to compare across a limited range of blink amplitude. Nevertheless, the data suggest that the difference in timing of airpuff- and light-evoked muscle activity results from activation through different sensory systems.

The integrated EMOO increases systematically as blink amplitude increases. Plots of normalized EMOO as a function of the amplitude of individual
Fig. 3A-C. EMG response to trigeminal and visual stimulation. A Lid position and the unrectified burst of EMG_{oo} obtained from Rabbit 4 during individual air- and light-evoked blinks. Calibration bars in parts A and C indicate 1 mm lid movement and 20 ms. B Rectified EMG records from Rabbit 5 show the decrease in EMG_{oo} and increase in EMG_{oo} during blinks. Increases in EMG activity are indicated by upward deflection of the trace; decreases in activity are indicated by downward deflection. Dashed vertical line marks the time of the peak in the initial OO burst during each blink. C Lid movement and unrectified EMG response in Rabbit 1 to supraorbital nerve stimulation (indicated by the arrow).

Fig. 4. EMG_{oo} response to change in stimulus intensity. Integrated, normalized data are from Rabbit 5 in response to 25 ms (diamonds) and 50 ms (stars) duration light flashes of varied luminance. The pair of diamonds indicates data collected at the beginning and at the end of the experiment.

blinks of all size indicate a similar, linear relation for both air- and light-evoked blinks. So, while the frequency of the burst of OO activity may be related to lid velocity, the total amount of OO activity appears to determine final downward lid displacement.

Stimulus-response characteristics: stimulus intensity

The primary determinant of the intensity of the blink-related EMG_{oo} and ultimately of the size of the blink is the intensity and duration of the blink-eliciting stimulus. For example, increasing the intensity of a light stimulus while holding stimulus duration constant results in a greater EMG_{oo} (Fig. 4). EMG_{oo} increases with increments in intensity over a wide range of luminance values. Given the correlation between blink amplitude and EMG_{oo} activity, it is not surprising that substituting blink amplitude for EMG_{oo} activity in this and similar plots yields a practically identical figure. A comparable increase in EMG_{oo} and blink amplitude occurs with increments in the intensity of a constant duration airpuff. Thus, EMG_{oo} activity and blink amplitude both correlate positively with stimulus intensity.
Changes in stimulus duration also systematically affect OO activity. EMG_{OO} increases with stimulus intensity for 25 ms and 50 ms light flashes, but the longer duration stimulus produces greater EMG response (Fig. 4). When stimulus intensity is held constant and stimulus duration varies, EMG_{OO} and blink amplitude increase in a similar manner in response to longer duration airpuffs or light flashes (Fig. 5A). Plots of blink amplitude versus stimulus duration produce an array of curves because individual rabbits vary in their relative response to stimuli and because rabbits were tested at different levels of intensity. Nevertheless, all of the curves in these plots show similarly shaped functions with a rapid increase in blink amplitude (or EMG magnitude) for shorter duration stimuli and a less rapid increase in amplitude for longer duration stimuli. In fact, the normalized EMG response for all subjects plotted as a function of stimulus duration yields a single curve, similar to that which would result if the data in Fig. 5A were normalized for amplitude and replotted. Thus, the blink response to air or light stimuli of varied duration changes in a regular fashion for all subjects.

Blink amplitude as a function of air or light stimulus duration consistently increases more rapidly for relatively short duration stimuli of either type than it does for longer duration stimuli. This occurs at all blink amplitudes, including small ones, which indicates that the plateau in amplitude is not due to the upper lid meeting the lower lid. Instead, this is the result of the neural program for generating blinks.

Plotting blink duration as a function of stimulus duration as shown for airpuffs in Fig. 5B provides insight into the reason for the change of slope. With stimulus durations shorter than 150 ms, blink duration remains nearly constant about 65 ms. Further increases in airpuff duration result in a sharp rise in blink duration. Blink duration increases in a qualitatively similar, two-part, manner with longer duration light stimulus, except that blink duration is approximately 120 ms with stimulus durations less than 50 to 75 ms and rises steeply as stimulus duration exceeds 75 ms. For both air and light, the values of blink duration across subjects are remarkably consistent despite differences in level of stimulus intensity and differences in the amplitude of the blink. Since the relation between stimulus duration and blink duration is independent of blink amplitude for brief stimulus durations, it is not surprising that most investigators report only a weak relation between blink amplitude and blink duration (Evinger et al. 1984; Hung et al. 1978; Kennard and Glaser 1984).

Considered as a whole, the data show that OO responses and corresponding lid movements occur in two discrete phases. As air or light stimulus duration increases from 0 ms to about 150 ms, the duration of the blink remains relatively constant while EMG_{OO} activity and blink amplitude increase rapidly. Then, with further increase in stimulus duration, blink duration increases considerably while EMG_{OO} activity and final blink amplitude exhibit only minor increases. This suggests that blink generation is a

**Stimulus-response characteristics: stimulus duration**

![Graph A](image1.png)  
**Fig. 5.** A Blink amplitude vs light flash duration. Data obtained from four rabbits (R2, R3, R4, R5) in five experiments in which light flash luminance was kept constant while flash duration varied. Luminance in foot-Lamberts equaled: 7565 for R2 (open star), R3 (solid star), and R4 (diamond), 2810 for R5 (circle with solid line), and 1330 for R5 (circle with dashed line). Each point in parts A and B represents the average of 8 to 10 blinks per rabbit. B Blink duration vs airpuff duration. Data obtained from four rabbits in five experiments in which air pressure was kept constant and airpuff duration varied. Pressure in lbs/sq in equaled: 17 for R2 (open star), 13 for R3 (solid star), 10 for R4 (diamond), 9 for R5 (circle with solid line), and 15 for R5 (circle with dashed line).
two-step process. First, in response to initial stimulation, a burst of OO activity of a preset frequency and duration is programmed. As long as the stimulus is relatively brief, increments in stimulus duration increase the intensity of EMG_{OO} activity, but not the duration of the activity, causing the resulting blink to grow in size. When the stimulus duration reaches a critical length, the blink generating neurons switch their mode of action. Instead of increasing the frequency of OO motoneuron activity, the duration of OO activity increases. This results in a regular lengthening of blink duration while increasing only slightly the amplitude of the blink.

Such an interaction between blink amplitude and blink duration is readily apparent with changes in stimulus duration, but not with changes in stimulus intensity. When air or light intensity increases, both blink amplitude and blink duration increase together at all levels of stimulus intensity used. This suggests that change in stimulus intensity involves a single process that affects blink amplitude and duration synchronously.

**EMG response to stimuli of varied intensity and duration**

The EMG activity recorded in response to stimuli of varied magnitude and duration is consistent with the preceding analysis. Airpuffs or light flashes of increasing intensity are associated with larger initial bursts of EMG_{OO} activity and longer decay times (Fig. 6A). Also note the steady change in the time to peak EMG_{OO} activity and in the duration of the lid movement associated with light flashes at three levels of intensity. The EMG records show the accompanying blink-related decrease in LP activity. There is a slight trend towards smaller decreases in EMG_{LP} with smaller blinks. Since the 25 ms flash ends before the lid begins to move (note the light artifact in the lid position traces), these blinks cannot depend upon sensory feedback. Each blink must be individually programmed in advance of the movement.

Air or light stimuli of increasing duration but constant intensity produce increasingly longer and larger bursts of EMG_{OO} activity (Fig. 6B). The
EMG$_{OO}$ response to the briefest stimulus depicted, a 50 ms light flash, is a single, sharp burst of activity that decays gradually. In response to the 100 ms stimulus, a similar initial burst occurs followed closely by an emerging second burst of activity. The response to the 125 ms stimulus begins with a burst that is also practically identical to the initial burst associated with the 50 and 100 ms flashes, but continues with a second burst of activity that is greater in both intensity and duration than that associated with the 100 ms stimulus. The amplitude of the initial burst reflects the intensity of the eliciting stimulus. This early burst, which represents the entire blink response to very brief stimuli and just the early response to longer duration stimuli, is a constant and for long duration stimuli no longer marks the time of the overall peak of the OO burst. Instead, the peak of EMG$_{OO}$ activity occurs at increasingly later times during the secondary burst. The secondary burst only begins to decay when stimulation is completed. Since the EMG$_{OO}$ response reflects the duration of the stimulus, the blink motoneurons must depend on current sensory information to maintain the blink. Thus, one blink pathway initiates OO motoneuron activity based on the intensity of the stimulus when stimulation begins. A second longer or slower pathway then maintains OO activity using current stimulus information. The decrement in EMG$_{LP}$ activity is similar for all blinks and is reminiscent of the response to stimuli of varied intensity.

Discussion

Eyeblinks of different forms

The lid kinematics and the patterns of EMG activity in the rabbit show two distinct classes of reflex blink. Air-evoked blinks achieve a higher maximum velocity and require less time for completion than equal amplitude light-evoked blinks. The two factors that appear to underlie this kinematic difference are the initial frequency of OO activity and the timing of activity in the reciprocally-acting lid muscles. The air-evoked EMG$_{OO}$ is initially more brisk than the light-evoked EMG$_{OO}$, and the LP relaxes before OO activation during air-evoked blinks, but remains active until after the OO burst begins during light-evoked blinks. Since the relation between integrated EMG$_{OO}$ and blink amplitude is similar for both light- and air-evoked blinks, the total amount of OO activity accompanying equal amplitude air- and light-evoked blinks is equivalent. This implies that an individual OO motoneuron emits higher firing frequencies for an air-elicited blink. But, since a light-elicited blink entails a longer duration of discharge, the OO motoneuron probably produces the same number of action potentials for air- and light-evoked blinks of equal amplitude. Medium-lead burst neurons, the premotor afferents of extraocular motoneurons that produce saccadic eye movements, exhibit a similar pattern of activity. During a saccade these normally quiescent neurons produce a high frequency burst of activity in which firing frequency correlates with maximum saccade velocity and the number of spikes in the burst correlates with saccade amplitude (Keller 1974; King and Fuchs 1979). So, blink-producing neurons may have properties similar to saccade-producing neurons.

The difference between air- and light-elicited blinks means that either the premotoneurons regulating LP and OO activity are separate, or that the sequence of events in a common set of premotoneurons must vary in response to the two types of stimuli. The supraorbital data suggest that, regardless of the mechanism, the difference is modality, rather than stimulus specific and categorization by modality may be the most useful way of grouping forms of reflex blink. Human blinks are kinematically similar to rabbit blinks (Evinger et al. 1984), involve the same afferent and efferent pathways, and preliminary data (Doane 1980; Manning and Riggs, unpublished data) suggests that different forms of blinks may also be present in humans.

Trigeminal and visual stimuli evoke downward excursions of the eyelid using the same set of muscles, but the movements are strikingly different. In the study of motor control, this is an example of muscle "synergy" or "form" of movement. The concept arose from the analysis of multijoint movements in which the central nervous system appears to simplify the control of movement by restricting itself to only a few of the possible patterns of muscle contraction capable of bringing the limb to a certain endpoint. Production of distinct forms of a movement can be accomplished by a shift in the relative timing of muscle contraction. The particular form of the movement that is elicited depends on the stimulus. For example, turtles scratch their bodies with three distinct hindlimb movements (Morita et al. 1985; Robertson et al. 1985), depending on the location of the irritant. The different forms of scratching result from variations in the timing of limb muscle contraction. Likewise, to restore balanced upright posture, human subjects evoke one of two movements that constitute different forms, ankle synergy or hip synergy (Nashner and McCollum 1985), depending on the base of support. Again, a shift in the timing of muscle contraction in the same set of muscles underlies these two synergies.
Blinks exhibit forms or synergies in a similar fashion. The kinematically distinct movements achieve the same end, lowering the eyelid, but they differ in the timing of lid muscle contraction, which depends on the nature of the stimulus. The relative simplicity of neural organization underlying blinks provides an ideal motor system in which to analyze the concept of muscle synergies at a cellular level.

**Stimulus control of blinking**

Despite the different forms of blinks evoked through visual and trigeminal afferents, all blinks share basic features. Blink amplitude and its primary determinant, OO activity, correlate positively with stimulus magnitude, a common feature of reflexes (e.g., Sherrington 1948). More importantly, two forms of neural control appear to operate during reflex blinks. The earliest component of the lid movement is programmed in advance of the movement. Regardless of the ultimate duration of the stimulus, the initial lid movement is the same for a stimulus of constant intensity. If the stimulus ends before blink initiation so that lid movement does not alter sensory input, the blink still begins in the same manner, but terminates after a set time. In this case the blink producing neurons program the entire blink, from start to finish, before initiating the movement. With stimuli of increasing duration, the period of OO activity lengthens. This implies that following the early, preprogrammed portion of the blink, automatic termination of the blink does not occur. Instead, lid closure comes under stimulus control. Final OO burst intensity and duration reflect stimulus intensity and duration.

This pattern of response, which starts with an unchanging, preset component and finishes with a more sensitive, adjustable component, is found in other reflexes, many of which like blinking (Evinger and Manning 1985) show adaptive learning. For example, the vestibuloculor reflex (VOR) exhibits a similar, two-part organization (Lisberger 1984) in which vestibular stimulation quickly evokes an initial compensatory eye movement followed by a secondary component of the movement 5 ms later. Changing the gain of the VOR systematically alters the second component, but not the first component. Such data suggest that the secondary component of the blink may turn out to be that portion of the blink reflex that is subject to modification through more central control.

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