Conditioned Eyelid Movement Is not a Blink

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Schrade Powers A, Coburn-Litvak P, Evinger C. Conditioned eyelid movement is not a blink. J Neurophysiol 103: 641–647, 2010. First published November 25, 2009; doi:10.1152/jn.00631.2009. Based on kinematic properties and distinct substrates, there are different classes of eyelid movement described as eyeblinks. We investigate whether the eyelid movements made in response to a conditioned stimulus (CS) are a category of eyelid movements distinct from blinks. Human subjects received 60 trials of classical eyelid conditioning with a tone as the CS and electrical stimulation of the supraorbital branch of the trigeminal nerve as the unconditioned stimulus (UCS). Before and after training, reflex blinks were elicited with the UCS. The kinematics of conditioned responses (CRs) differed significantly from those of reflex blinks. The slope of the amplitude-maximum velocity function was steeper for reflex blinks than for CRs, and reflex blink duration was significantly shorter than CR duration. Unlike reflex blinks, for which maximum velocity was independent of blink duration, the maximum velocity of CRs depended on CR duration. These quantitative and qualitative differences indicated that CRs were a unique class of eyelid movements distinct from blinks and eyelid movements with vertical saccadic gaze shifts.

INTRODUCTION

Eyeblink is used to describe several types of eyelid closures. It can refer to the unconscious spontaneous blinks that mammals make several times a minute (Stern et al. 1984) and reflex blinks elicited by corneal irritation and periorbital stimulation (Doane 1980). Investigators frequently employ the term eyelid to describe lid closures made in conditioned learning paradigms (Thompson and Krupa 1994; Thompson et al. 1997). Describing these distinct lid closures under a single term implies that they possess the same characteristics and neural bases. If they are different types of lid movements, however, then putting them under the same physiological umbrella potentially confuses data interpretation. We know that there are distinct classes of eyelid movements just as there are distinct types of eye movements (Leigh and Zee 2006). For example, it is clear that blinks are distinct from the eyelid movements that accompany saccadic vertical gaze shifts as determined by their kinematics and neural bases (Evinger et al. 1991; VanderWerf et al. 2003). Previous studies in animals report that the latency and topography of conditioned responses (CRs) are different from those of reflex blinks in animal models (Thompson and Krupa 1994 for review) and that there are significant kinematic differences between reflex blinks and CRs (Gruart et al. 2000). These data suggest that CRs and blinks are discrete classes of eyelid movement in animals. The question investigated in this study on human subjects is whether CRs have kinematic properties similar to reflex blinks or whether they are a unique type of eyelid movement.

Different categories of eye movements can be distinguished by their kinematic attributes and neural substrates (Leigh and Zee 2006). For example, saccadic eye movements possess a characteristic relationship between saccade amplitude and the maximum velocity achieved during the saccade, the “main sequence” (Leigh and Zee 2006). Reflex, voluntary, and spontaneous blinks exhibit an equivalent main sequence in which maximum lid velocity increases monotonically with blink amplitude (Baker et al. 2002; Bour et al. 2000; Evinger et al. 1984, 1991; Guitton et al. 1991; Horn et al. 1993; Koroscik et al. 2006; VanderWerf et al. 2003). As with saccadic eye movements (Leigh and Zee 2006), the amplitude-maximum velocity relationship for blinks is normally invariant but can change with neurological conditions (Abell et al. 1998; Schicatano et al. 2002; Sibony et al. 1991), drugs (Small et al. 1995), and drowsiness (Schleicher et al. 2008). Thus if CRs are blinks, then they should exhibit the same amplitude-maximum velocity relationship as blinks. Conversely, significant differences between CR and reflex blink kinematics would indicate that CRs are a different type of eyelid movement from blinks.

METHODS

Nine subjects aged 19–48 (2 males, 7 females) participated in the study. All subjects gave informed consent for their participation. All experiments were performed in strict accordance with federal, state, and university regulations regarding the use of humans in experiments and received approval of the University Institutional Review Board.

Although species with a moveable nictitating membrane, e.g., rabbits, exhibit eye retraction and concomitant nictitating membrane extension with CRs (McCormick et al. 1982), we focused on the eyelid movement in humans because their nictitating membrane does not move, and their eye retraction is difficult to measure noninvasively (Evinger et al. 1984). We measured upper eyelid movement using the magnetic search coil procedure and recorded concomitant orbicularis oculi electromyographic (EMG) activity (OOEMG) from both eyelids (Evinger et al. 1991). To monitor upper eyelid position, a 30-turn coil (2 mm diam, 25 mg weight) was taped to the center of the lower margin of the upper eyelid. The subject sat within a magnetic field. As reported by previous investigators (Evinger et al. 1991; Guitton et al. 1991; Sun et al. 1997; VanderWerf et al. 2003), this procedure does not interfere with eyelid movement or cause discomfort in human subjects. The OOEMG was recorded through two miniature silver plates (≤2 mm diam) taped to the lateral and medial portion of the upper eyelid. The OOEMG signal was amplified and filtered from 0.3 to 5 kHz. An electrode on the forehead served as ground.

The unconditioned stimulus (UCS) was a 170-μs duration constant current stimulus to the supraorbital branch of the trigeminal nerve (SO) delivered through a pair of 1-cm gold-plated electrodes (Evinger et al. 1991). After identifying the threshold stimulus current sufficient to evoke a blink reliably, SO intensity was set at 2.5 times this threshold to serve as the UCS evoking reflex blinks. This intensity was not an aversive stimulus, and no subject reported the stimuli to be
uncomfortable. The experience of the authors is that stimuli at this intensity feel like a tap to the forehead. To elicit painful sensations in humans requires stimulus intensities of approximately five times threshold (Ellrich et al. 2001). Across all subjects, threshold SO current ranged from 1.0 to 2.0 mA.

The subjects underwent classical conditioning using a delay procedure. The CS was a 500-ms 1,000-Hz tone (80 dB SPL) presented through a loudspeaker located 2 m away from the subject’s head. The UCS occurred simultaneously with the end of the CS. Sixty CS-UCS conditioning trials were given with a variable 20/5-s intertrial interval. A CS-alone trial and a UCS-alone trial were presented after every block of 10 conditioning trials. Before and after conditioning trials, 20 UCS-alone reflex blinks were collected. We determined reflex blink kinematics from this preconditioning data and from UCS-alone presentations within each block. We defined CRs as lid closures of ≥1° that occurred after the first 100 ms of the CS during both CS-UCS trials and CS-alone trials. CR kinematics were established from these data. CR latency was calculated as the time after CS onset that the CR began. All subjects watched a videotape during the experimental session to maintain alertness. Subjects were not told that the study investigated classical conditioning but were told that they would receive shocks and hear tones during the experiment.

**RESULTS**

We reasoned that subjects who blinked on a high percentage of early trials were probably blinking voluntarily instead of reflexively. The experience of the authors is that stimuli at this intensity feel like a tap to the forehead. To elicit painful sensations in humans requires stimulus intensities of approximately five times threshold (Ellrich et al. 2001). Across all subjects, threshold SO current ranged from 1.0 to 2.0 mA.

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making conditioned eyelid movements. Therefore we included only subjects who showed lid closures during the CS on <60% of the first block of 10 trials in our analysis of CRs. Two of the nine subjects made lid closures on 6 or 9 of the first 10 trials and were not included for further data analysis of CRs. The seven remaining subjects made <60% CRs in the first block. As with previous studies of human eyelid conditioning (Sears et al. 1994; Topka et al. 1993; Woodruff-Pak and Thompson 1988), these seven subjects significantly increased the proportion of CRs across the 60 trials [Fig. 1A, black circle; F(5,35) = 5.2, P < 0.001]. On the average, these subjects achieved seven CRs in 10 trials by the fourth block. The CRs began just before the UCS over the 60 trials, and CR latency did not change significantly [Fig. 1B, black circle; F(2,170) = 0.76, P > 0.05]. Averaged over all seven subjects, the mean CR latency from CS onset during the first 20 trials was 411.7 ± 11.9 and 398.9 ± 8.4 ms for the last 20 trials, the largest proportion of CRs beginning just before the UCS (Fig. 1C, solid line). Typically, the CR continued through the UCS (Fig. 3, A and B). In CS-alone trials, lid closure began during the CS and peaked after the CS ended either just after or coincident with the time the reflex blink reached maximum lid closure on trials with a UCS (UCR; Fig. 1D). These latencies were similar to those obtained in another laboratory using the same UCS (Sommer et al. 1999).

The proportion of CRs and their latency were significantly different, however, for the two subjects who made ≥60% CRs on the first block of trials. These subjects did not exhibit a significant increase in CR probability across trials [Fig. 1A, white circle; F(5,12) = 2.6, P > 0.05], achieving seven CRs in 10 trials in the first and second training blocks. For these two subjects, CR latency from CS onset decreased significantly across training [Fig. 1B, white circle; F(2,96) = 7.93, P < 0.001]. The average CR latency during the first 20 trials was 332.6 ± 14.4 ms. CR latency was significantly shorter in the second (264.8 ± 12.2 ms; P < 0.002) and third (264.8 ± 14.2 ms; P < 0.002) blocks. By the last block, the lid was already opening when the UCS occurred rather than closing (Figs. 1E and 3C). This distribution of CR latencies was significantly different from that of the other seven subjects [Fig. 1C; F(1,96) = 48.8, P < 0.001]. In CS-alone trials, lid closure peaked during the CS, well before the UCR would have occurred (Fig. 1E). These results suggested that the two subjects with 60% CRs in the first block responded to CS onset rather than to the time of UCS because lid closure with the CS moved closer to CS onset and away from the time of the UCR. Thus the two subjects making 60% CRs in the first block appeared to make voluntary blinks in response to the CS rather than CRs initiated by the CS.

We characterized the kinematics of upper lid closure during the CS and reflex blinks using lid movement amplitude, maximum velocity, and duration (Fig. 2). The amplitude of lid closure was the difference between initial lid position and maximal lid closure (Fig. 2A, Amp). On CS-UCS trials when the CR blended into the UCR (Fig. 3, A and B), we defined maximum lid closure as the lid position immediately before the beginning of the UCR. Maximum velocity was the peak velocity achieved during lid closure (Fig. 2, Peak Vel). We calculated duration as the time between the start of lid closure when the lid velocity exceeded 5% of maximum lid velocity and the time of maximum lid closure on CS-alone trials (Fig. 2, Dur).
lid velocity further illustrated the increased reflex blink lid closing velocity (Fig. 2C, gray line) relative to that of the slightly larger CR (Fig. 2C, black line). Consistent with the lower peak velocities, CR closing phase duration (258 ms) was longer than reflex blink closing phase duration (50 ms) in this example. Dissimilarities between the pattern of OOemg activity producing the CR and the reflex blink accounted for these kinematic differences (Figs. 2 and 3A). As the sum of OOemg activity determines lid closure amplitude (Domingo et al. 1997; Evinger et al. 1991; Gruart et al. 2000), the integrated OOemg activity for the reflex blink was ~70% as large as the CR integrated EMG illustrated in Fig. 2. As lid closure duration is a function of OOemg duration (Evinger et al. 1991), the CR OOemg had a longer duration than that of the reflex blink. Consistent with the correlation between peak OOemg magnitude and maximum velocity (Evinger et al. 1991), the peak OOemg of the reflex blink was 2.4 times larger than the CR peak OOemg for the examples in Fig. 2. This pattern of low-velocity, long-duration CRs was present throughout training (Fig. 3B) for all seven subjects. The dissimilar patterns of OOemg activity and resulting kinematic differences between CRs and reflex blinks suggested that different neural processes produced these two types of eyelid movements.

CR kinematics were significantly different from reflex blink kinematics for the seven subjects who exhibited CRs (Fig. 4, A and B, conditioned subjects), but not for the two subjects who failed to condition (Figs. 3C and 4, C and D, unconditioned subjects). Although maximum velocity increased with lid closure amplitude for both CRs and reflex blinks, CR maximum velocity was always less (Fig. 4A, ○) than the maximum velocity of equal amplitude reflex blinks (Fig. 4A, ●) in the subjects who conditioned. The slope of the amplitude–maximum velocity relationships was significantly steeper for reflex blinks than for CRs [t(6) = 5.15, P = 0.002]. For the subjects who failed to condition, however, the slope of the amplitude–maximum velocity relationship for lid closures during the conditioned stimulus (○) and reflex blinks (●) were not significantly different [Fig. 4C, t(2) = 1.17, P > 0.05].

CR and reflex blink durations were also significantly different for the seven subjects exhibiting conditioning. A Tukey post hoc analysis of an ANOVA of CR and reflex blink durations revealed that CR duration (113.7 ± 73.3 ms) was significantly longer than reflex blink duration (55.4 ± 21.8 ms; P < 0.001 Fig. 4B). CR duration was also more variable than reflex blink duration. The coefficient of variation for movement duration was 0.43 for reflex blinks but twice as large for CRs (0.86). For the two subjects who did not condition, however, a Tukey post hoc analysis showed that there was no significant difference between lid closure duration during the CS (Fig. 4D, ○) and reflex blink duration (Fig. 4D, ●). Post hoc analysis also showed that there was no difference between lid closure duration for the two subjects who did not condition and the reflex blink duration of the seven subjects exhibiting conditioning. Variability of the duration was similar for lid closure during the conditioned stimulus and reflex blinks of the two subjects who did not condition; the coefficient of variation for lid closure duration during the CS and reflex blinks was 0.43 and 0.45, respectively. The coefficient of variation for lid closure duration during the CS for the two subjects who didn’t condition was identical to the reflex blinks of the seven subjects who did condition (0.43).

Because human reflex blink duration only changes slightly for amplitudes >5° and amplitude strongly predicts maximum velocity (Fig. 4, A and C) (Evinger et al. 1991), it follows that maximum lid velocity should not correlate well with blink duration. If CRs are blinks rather than a separate class of eyelid

**FIG. 4.** Lid kinematics. A: the relationship between amplitude and maximum velocity for CRs (○) and RBs (●) averaged over all 7 subjects exhibiting conditioning. B: the relationship between amplitude and duration for CRs (○) and RBs (●) averaged over all 7 subjects exhibiting conditioning. C: the relationship between amplitude and maximum velocity for lid movements made during the CS (○) and RBs (●) averaged over the 2 subjects who did not condition. D: the relationship between amplitude and duration for lid movements made during the CS (○) and RBs (●) averaged over the 2 subjects who did not condition. Error bars are SE.
movements, then there should be no consistent relationship between CR duration and maximum velocity. Pooling all of the CR data from the seven subjects exhibiting CRs, we calculated average maximum velocity as a function of reflex blink (Fig. 5A, reflex blink) and CR (B, CR) durations between 45 and 110 ms. There was no relationship between maximum velocity and duration for reflex blinks \([r_{(34)} = 0.254, P > 0.05]\), but maximum velocity clearly increased with duration for CRs \([r_{(14)} = 0.626, P < 0.02]\).

**DISCUSSION**

Blinks and the eyelid movements accompanying saccadic vertical gaze shifts are two classes of eyelid movements previously differentiated by their distinct kinematics and neural substrates. For reflex, voluntary, and spontaneous blinks, there is a consistent linear relationship between blink amplitude and maximum velocity analogous to saccadic eye movements (Evinger et al. 1991; Guitton et al. 1991; Korosec et al. 2006; Sun et al. 1997; Trigo et al. 2003; VanderWerf et al. 2003). The eyelid movements with saccadic vertical gaze shifts, however, are kinematically different from blinks (Fig. 6). Relative to blinks, downward saccadic lid movements achieve lower velocities (Fig. 6A, \(\bullet\) vs. \(\triangle\)) and have longer durations (B, \(\bullet\) vs. \(\triangle\)). This kinematic difference occurs because the lid movements with downward gaze shifts primarily result from the passive properties of the eyelid (Becker and Fuchs 1988; Evinger et al. 1991; Guitton et al. 1991; Korosec et al. 2006; Manning et al. 1990; Sibony et al. 1991). Further evidence that blinks and lid movements with vertical saccades are discrete classes of lid movements is that the neural substrates that support the two lid movement types differ. For example, seventh nerve palsy disrupting innervation of the lid closing orbicularis oculi muscle severely impairs blinking but does not alter the eyelid movements accompanying vertical eye movements (Leal-Campanario et al. 2004; Manning et al. 1990; Sibony et al. 1991; VanderWerf et al. 2007). Lesions affecting the mesencephalic reticular formation M group can disrupt lid movements with vertical saccades without affecting blinks or saccadic eye movements (Galetta et al. 1996; Horn and Buttner-Ennever 2008; Horn et al. 2000). Thus these two categories of eyelid movements are kinematically distinct and arise through separate neural substrates. Although their neural basis has not been identified, another type of kinematically distinct movement is the emotional eyelid movement (Gruart et al. 1996).
amplitudes but similar at large amplitudes (Fig. 6). However, is longer than that of downward lid saccades for small amplitudes. These kinematic dissimilarities probably occur because of the passive nature of downward lid saccades and differences in the neural substrates for these two types of lid movements.

CRs are also distinct from downward saccadic lid movements. The maximum velocity of CRs is faster than equivalent amplitude downward saccadic lid movements, particularly at larger amplitudes (Fig. 6A, ○ vs. ●). The duration of CRs, however, is longer than that of downward lid saccades for small amplitudes but similar at large amplitudes (Fig. 6B, ○ vs. ●). These kinematic dissimilarities probably occur because of the passive nature of downward lid saccades and differences in the neural substrates for these two types of lid movements.

Just as different neural circuits create lid movements with vertical saccades and reflex blinks, the neural circuits supporting CRs and reflex blinks are distinct. Inactivating the inferior olive blocks CR acquisition but has no consistent effect on reflex blinks (McCormick et al. 1985; Pellegrini and Evinger 1997; Thompson et al. 1997; Welsh and Harvey 1998; Yeo et al. 1986). Damage to the medulla dorsolateral to the inferior olive, however, severely affects trigeminal reflex blinks but is not reported to affect CRs (Cruccu et al. 2005).

The physiology and anatomy of the cerebellar interpositus (IP) nucleus also reveal neural differences between CRs and reflex blinks. Evidence from IP recordings indicates that there are two anatomically adjacent but physiologically distinct populations of eyelid-related IP neurons. A primarily posterior IP group, pause neurons, modulates the duration and amplitude of trigeminal reflex blinks and is essential for blink adaptation, whereas the more rostral eyelid-related IP neurons, burst neurons, do not modify reflex blinks (Chen and Evinger 2006). These neurons are in the IP region associated with CRs (Aksenov et al. 2004, 2005; Delgado-Garcia and Gruart 2002, 2005; Freeman et al. 2005; Gruart et al. 1997; Jimenez-Diaz et al. 2002, 2004). Correlating the two categories of IP neurons with two different types of eyelid movements, blinks and CRs, eliminates the argument about whether the loss of CRs following an IP lesion is a memory loss or a performance deficit. Some investigators describe a CR loss with a smaller effect on reflex blinks (Bracha et al. 1994; Jimenez-Diaz et al. 2004; Welsh 1992; Welsh and Harvey 1989). Other investigators report a loss of CRs with no change in reflex blinks (Ivkovich et al. 1993; McCormick and Thompson 1984; Steinmetz et al. 1992). These divergent results may arise from differences in the anterior-posterior extent of IP lesions and the collection of data immediately after IP inactivation (Bracha et al. 1994; Jimenez-Diaz et al. 2004) rather than days after the lesion (Ivkovich et al. 1993; McCormick and Thompson 1984; Steinmetz et al. 1992). Linking the two types of IP neurons to two distinct classes of eyelid movements makes it clear that IP lesions can affect reflex blinks as well as CRs. The IP is critical for CRs (De Zeeuw and Yeo 2005; Thompson 2005) but only modulates reflex blinks (Chen and Evinger 2006; Jimenez-Diaz et al. 2004). It is reasonable that the cerebellum can be critical for memory and production of CRs while simultaneously modulating reflex blinks. Thus CRs and reflex blinks appear to be controlled through parallel cerebellar circuits, consistent with the other evidence that CRs and blinks are functionally and neuronally discrete classes of eyelid movements.

The distinctions between blink and CR eyelid movements are analogous to those between saccadic and smooth pursuit eye movements in many ways. For example, both saccades and blinks undergo rapid adaptation when the saccade or blink falls short of its target (Chen and Evinger 2006; Evinger and Manning 1988; Hopp and Fuchs 2004; Pellegrini and Evinger 1997; Wallman and Fuchs 1998). Although people easily generate voluntary saccadic eye movements and blinks, it is very difficult to produce voluntary smooth pursuit eye movements (Krauzlis 2004; Leigh and Zee 2006) or voluntary CRs (Marquis and Porter 1939). People begin initiating anticipatory smooth pursuit eye movements following repeated presentations of a transient target movement (Barnes and Schmid 2002; Barnes et al. 2002). This pattern of smooth pursuit is remarkably similar to CRs that develop with eyelid conditioning. Like the loss of CRs and the disruption of blink amplitude following a cerebellar lesion (Bracha et al. 1994; Jimenez-Diaz et al. 2004; Steinmetz et al. 1992), smooth pursuit is lost, whereas saccadic eye movements are only dysmetric with cerebellar lesions (Leigh and Zee 2006).

Like the eye movement system, eyelid control appears to utilize discrete classes of eyelid movements to accomplish its goals. These different types of eyelid movements separate themselves based on their kinematics and neural substrates. Blinks, eyelid movements with vertical saccadic gaze, and conditioned eyelid movements appear to serve different functions for the eyelid control system.

Acknowledgments

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