To blink or not to blink: inhibition and facilitation of reflex blinks

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Abstract A reflex blink typically inhibits subsequent blinks. In this study, we investigated whether the nature and time course of this inhibition vary when different combinations of blink-evoking stimuli are used. We used the paired stimulus paradigm, in which two blink-evoking stimuli – a conditioning stimulus followed by a test stimulus – are presented with a variety of interstimulus intervals, to examine the interactions between blinks evoked by trigeminal and acoustic stimuli in rats and humans. In addition, we studied the effect of a blink-evoking trigeminal stimulus on subsequent gaze-evoked blinks in humans. The results revealed that long-lasting inhibition occurred when the conditioning and test stimuli were within the same modality. A shorter period of inhibition followed by facilitation occurred when the stimuli were in different modalities. The data demonstrate that a blink-evoking stimulus initiates a lengthy period of inhibition in its own sensory pathway and a shorter period of inhibition in the reticular formation and/or in blink motoneurons. In addition, the results show that the blink-evoking stimulus also initiates a facilitatory process. Thus, the magnitude of a blink reflects a balance between inhibitory and facilitatory processes.

Key words Reflex blinks · Trigeminal · Auditory · Startle · Prepulse

Introduction

A critical feature of the blink motor program is that it must inhibit itself following a blink. With each lid movement of a blink, air races through the eyelashes and the lid rubs against the cornea. Presentation of either of these stimuli is sufficient to elicit a reflex blink. Thus, if a blink or the stimulus that evokes it fails to initiate a period of inhibition, then each blink will elicit a reflex blink, starting blepharoclonus or a spasm of lid closure. The current study investigates the duration and sites of this inhibition by pairing reflex blinks elicited by stimuli in the trigeminal and acoustic modalities and gaze-evoked blinks.

The paired stimulus paradigm provides a measure of the blink refractory period. For example, presenting pairs of identical stimuli to the supraorbital branch of the trigeminal nerve evokes two responses that normally differ markedly in amplitude. With interstimulus intervals less than 1500 ms, the blink evoked by the second (test) stimulus is smaller than the blink evoked by the first (conditioning) stimulus in humans (e.g., Kimura 1973a,b) and rodents (Basso et al. 1993; Pellegrini and Evinger 1995). Pellegrini and Evinger (1995) demonstrated that the suppression of the blink evoked by the second SO stimulus occurs within the trigeminal complex. If blink inhibition takes place only within the sensory nucleus active in producing a reflex blink, then there will be no inhibition of subsequent blinks elicited through a different stimulus modality.

In the present study, we investigated the interactions between blinks evoked by SO stimuli, acoustic stimuli, and gaze-evoked blinks. The results revealed that the conditioning stimulus or the blink it elicited caused a long-lasting inhibition of subsequent blinks evoked by test stimuli in the same modality. In contrast, the same conditioning stimulus or blink caused only a short-lasting inhibition of subsequent blinks evoked by a test stimulus in a different sensory modality. These data showed that there are at least two sites of blink inhibition. A
The subjects participated in every condition. The four classes of pairing joined a connector. Rats were alert and eating within 24 h of the stimulus evoked by an SO stimulus. To obtain control records, the subjects received a blink-evoking acoustic stimulus followed by an acoustic-acoustic condition. (3) The subjects received a pair of identical stimuli (SO-SO condition). (2) The subjects received a pair of identical stimuli. Not all subjects received the stimuli pairings were presented in separate sessions. Not all subjects participated in every condition. The four classes of pairing were: (1) The subjects received a pair of identical SO stimuli (SO-SO condition). (2) The subjects received a pair of identical blink-evoking acoustic stimuli (Acoustic-Acoustic condition). (3) The subjects received a blink-evoking acoustic stimulus followed by an SO stimulus. To obtain control records, the subjects received the SO stimulus alone on alternate trials (Acoustic-SO condition). (4) The subjects received an SO stimulus followed by a blink-evoking acoustic stimulus. To obtain control records, the subjects received the acoustic stimulus alone on alternate trials (SO-Acoustic condition). Interstimulus intervals (ISIs) in the above conditions ranged from 50 to 2000 ms. To diminish habituation, trials occurred every 30±5 s. To minimize changes in attention, human subjects read during the experiments.

For both human and rat subjects, we designated the reflex blink-evoking stimulus to SO stimulation as the intensity required for an SO stimulus to evoke OOemg activity on 50% of the trials. SO stimulus intensity was adjusted to approximately 2 times the blink threshold. At intensities greater than 1.25 times threshold, subjects responded on 100% of the trials. For humans, stimulus intensity ranged from 2.0 to 9.0 mA with stimulus durations of 150–200 μs. For rats, stimulus intensities ranged from 0.5 to 2.0 mA with stimulus durations of 60–100 μs. Acoustic stimuli were pure tones (1 or 2 kHz) presented through a speaker 0.5 m from the subject.

Stimulus duration was 50 ms for humans and 20 or 50 ms for rats, with a rise time of 0.1 ms and an intensity measured at the subject of 95 dB.

Gaze-evoked blinks

To investigate a blink that did not arise via the acoustic or trigeminal modalities, we tested the interaction between SO-evoked reflex blinks and gaze-evoked blinks in humans. Gaze-evoked blinks occur because they are a component of the command for saccadic gaze shifts (Evinger et al., 1994). Subjects fixated a central target 57 cm away. At the sound of a weak tone, they used a combined eye and head movement to acquire a continuously visible peripheral target 65° away from the fixation target as rapidly as possible. This movement elicited a gaze-evoked blink. On random trials, we presented an SO stimulus after the tone but before the subject began the head movement. We measured head position with a linear, low-torque potentiometer attached to a helmet that was securely affixed to the subject’s head.

Measurement and analysis of responses

The OOemg was amplified and filtered (0.3–5 kHz) and fed to a computer that digitized the records at 4 kHz and stored them for off-line analysis. The off-line analysis program integrated the OOemg activity and calculated the latency for the averaged components. For the gaze-evoked blink experiments in humans, we digitized both head position and OOemg at 5000 Hz. For each trial, the computer marked the beginning and end of the gaze-evoked blink and the head movement. For a pair of identical SO or auditory stimuli, we calculated a ratio of the integrated response to the second (test) stimulus divided by the integrated response to the first (conditioning) stimulus. Data for the responses evoked by paired stimuli of different modalities were calculated as the amplitude of response to a stimulus of the same modality when it was presented alone (control). Scatter plots showing the test/condition ratio at each ISI were fitted with a logarithmic curve. Logarithmic fits were slightly better than exponential and linear fits of the same data.

Results

Pairs of identical stimuli

SO-SO stimuli

Presenting pairs of identical SO stimuli dramatically altered the response to the second stimulus relative to the