ABSTRACT

Gaze-Evoked Blinks in Rhesus Monkeys

Gaze-evoked blinks, blinks that occur during rapid movements of the head and eyes, are believed to be the result of a shared mechanism that is responsible for a blink occurring with a saccade. In humans, it has been found that blinks are more likely to occur with larger saccades. Saccades accompanied with a blink are also more likely when attentional demands are low. Saccades associated with a reflex blink elicited by an air puff in monkeys have been shown to be slower than saccades without a blink. The purpose of the present study was to see if monkeys tested on visually-guided and memory-guided saccade tasks would show the same behavior in gaze-evoked blinks as humans. In this study, similar findings were found of gaze-evoked blinks in monkeys as were found in humans. Gaze-evoked blinks also slowed saccades as was found in reflex blinks elicited by a puff of air.

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Gaze-Evoked Blinks in Rhesus Monkeys

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ABSTRACT
Gaze-evoked blinks, blinks that occur during rapid movements of the head and eyes, are believed to be the result of a shared mechanism that is responsible for a blink occurring with a saccade. In humans, it has been found that blinks are more likely to occur with larger saccades. Saccades accompanied with a blink are also more likely when attentional demands are low. Saccades associated with a reflex blink elicited by an air puff in monkeys have been shown to be slower than saccades without a blink. The purpose of the present study was to see if monkeys tested on visually-guided and memory-guided saccade tasks would show the same behavior in gaze-evoked blinks as humans. In this study, similar findings were found of gaze-evoked blinks in monkeys as were found in humans. Gaze-evoked blinks also slowed saccades as was found in reflex blinks elicited by a puff of air.

INTRODUCTION
Saccadic gaze shifts, which are rapid reorientations of the head and eyes, are known to often be associated with blinks. These blinks, which occur through a contraction of the muscle orbicularis oculi, have been termed gaze-evoked blinks by Evinger et al. (1994). This term, gaze-evoked blinks, is used to distinguish them apart from reflexive blinks which can be elicited by a puff of air. A burst of activity in the lid-
closing orbicularis oculi muscle and a pause of tonic activity in the lid-raising levator palpebrae muscle occur during a blink (Evinger 1995, as cited in Goossens and Van Opstal 2000). Two theories have been postulated to explain the phenomenon of the close association between saccadic gaze shifts and blinks. One hypothesis is that the blinks are reflexive in nature and that they result from wind rushing across the cornea as it moves or the movement of air across the eyelashes as the head and eyes rotate (Evinger et al. 1994). The other hypothesis is that there is a connection in the neural circuitry between saccadic gaze shifts and blinking (Evinger et al. 1994). Some observations that have suggested such a link have been with patients that have certain neurodegenerative diseases who show only abnormal saccades when paired with a blink (Hain et al. 1986, as cited in Evinger et al. 1994). Other patients with a neurodegenerative disease can only make a saccade when a blink co-occurs (Leuzzi 1993, as cited in Evinger et al. 1994).

Blinks are accompanied by specific eye movements, particularly upward and abducting rotations of the eye when a blink occurs (Evinger et al. 1984). During a blink the eye also retracts inward (Evinger et al. 1984). It has been suggested that blink closing muscle activation, as described above, may be due to a specific input for blinks to the extraocular motorneurons (Evinger and Manning 1993, as cited in Goossens and Van Opstal 2000). Others have advocated that there is a combination of visual input and extraretinal factors that work in conjunction to provide accurate saccades that are paired with a blink (Guthrie et al. 1983; Hallett and Lightstone 1976, as cited in Goossens and Van Opstal 2000; Sparks and Mays 1983, as cited in Goossens and Van Opstal 2000). Evidence has also shown that the gaze shift and the blink system work reciprocally, where one can activate the other (Evinger et al. 1994).
In a study by Evinger et al. (1994), they showed that the amount of EMG activity, as well as the probability of activity, of the orbicularis oculi increased as the amplitude of the head movements in a gaze shift increased. When there was no movement of the head, a small activation of the orbicularis oculi could be measured during the saccade to the target. Interestingly however, they found that a large blink followed the initial saccade to the target during the returning saccade to the area of fixation (the area that must be stared at before the initiation of a trial). The size and probability of a blink was then speculated by Evinger et al. (1994) to be associated with how important the subject thought making the saccade to the target was. Through this study it was also concluded that it is unlikely that blinks occur with gaze shifts due to a reflex in response to wind against the eye or eyelashes. This conclusion was reached after it was found that many blinks were actually initiated before the movement of the head. To further investigate, they studied the orbicularis oculi EMG activity while the participant made a horizontal gaze shift with their eyes closed. In these trials, it eliminates the possibility of air blowing over the cornea of the eye, yet they found that there was a burst of activity from the orbicularis oculi on every saccadic gaze shift. They explained the phenomenon of the orbicularis oculi activity on every trial as the result of a possible increase in baseline activity that is caused by the eyelids already being closed.

In a study by Williamson et al. (2005), they tested in head-stabilized humans whether the fewer number of gaze-evoked blinks and the smaller activity of the orbicularis oculi found in the study by Evinger et al. (1994) were due to the visual stimulus or some other extraretinal factor. They tested this by having the participants make eye movements to a visible or previously visible stimulus. Two saccade tasks were
administered. One of the saccade tasks was a visually-guided, delayed saccade task (where the saccade was made to a visible target) and a memory-guided, delayed saccade task (where the saccade was made to a previously visible target) (Hikosaka and Wurtz 1983, as cited in Williamson et al. 2005). They found similar results in both the visually-guided and memory-guided tasks. The first saccade to the target (whether visible or previously visible) was not associated with a blink. However, the return saccade to the fixation area (refixation saccade) was accompanied by large orbicularis oculi activity. They concluded that the visual stimulus is not in itself needed to reduce the activity of the orbicularis oculi during a saccade and that it most likely comes from an extraretinal source. It was also stated that this difference in activity between the saccades to the target and the fixation area could be due to attentional factors seeing as there was no need for accuracy during the refixation saccade.

The present study sought to see if the previous findings in humans occurred in rhesus macaque monkeys (Macaca mulatta). Specifically, that greater orbicularis oculi activity was associated with larger saccades (Evinger et al. 1994) and that blinks were more common when attentional demands were reduced, during the refixation saccade (Williamson et al. 2005). The monkeys were tested using visually-guided and memory-guided saccade tasks.
METHODS

Subjects

Three male rhesus macaque monkeys (Macaca mulatta) with implanted eye coils were used in the study. Each was trained to perform visually-guided and memory-guided saccade tasks.

Behavioral tasks

Each monkey’s head was restrained and they were seated in a primate chair. Both the visually-guided and memory-guided saccade tasks began by having the monkey fixate on a point at the center of the screen for 500 to 1500 milliseconds (ms). A target point would then appear at various spots 6° or 18° from the fixation point. In the visually-guided saccade task (Fig. 1A, modified from Williamson et al. 2005), the target point would remain visible for a period of 800 to 1200 ms. In the memory-guided saccade task (Fig. 1B, modified from Williamson et al. 2005), the target point would flash for 200 ms and then disappear. The monkey, when cued, would then have to make a saccade to where the target used to be. The visually-guided and memory-guided trials were randomly interleaved. Each session consisted of 300 to 400 correct trials. The cue for the monkey to make the saccade to the target point was the fixation point disappearing, which the monkey then had 200 ms to make a saccade. In order for the saccade to be considered correct and the trial be included in analysis, the monkey had to be within 2° of the target point. The time between trials was 1500 to 2000 ms. To detect blinks, a small custom-made eye coil was taped to the left eyelid of the monkey.
**Fig. 1.** (modified from Williamson et al. 2005). Visually-guided and memory-guided saccade task.

**Data analysis**

The probability of blinks occurring, as well as their amplitude, was calculated. The amplitude and velocity of saccades were also calculated. Saccade velocity was often interrupted by blinks. To account for this, the mean polar velocity of each saccade was calculated. For the saccades that were not accompanied by a blink, the mean polar velocity was calculated 40 ms from the initiation of an eye movement. For the saccades that were accompanied by a blink, which are longer in latency (Goossens and Van Opstal 2000), the mean polar velocity was calculated 150 ms from the initiation of the eye movement.
RESULTS

Our results for gaze-evoked blinks in rhesus monkeys mirrored those found in humans. There was a significant difference between blinks occurring during saccades to the target and during refixation saccades ($p<.05$) (Fig. 2). Blinks were more likely to occur during the refixation saccade than during saccades to the target (Fig. 3). These results were found in both the visually-guided and the memory-guided saccade tasks. This is most likely due to the reduced amount of attentional demands during the refixation saccades.

![Monkeys](image)

Fig. 2. The percent of trials that had a blink occurring with a saccade to either the target or refixation.
Fig. 3. Shows a blink occurring during refixation saccade with eye positions (left) and polar eye position with polar saccade velocity (right).

It was also found that saccades that occurred with a blink were significantly larger than those that did not have a blink associated with them (Fig. 4). Also, saccades associated with a blink were slower than those that were not (Fig. 5).

Fig. 4. Mean amplitude of saccades with a blink and without a blink.
DISCUSSION

The results of the present study of gaze-evoked blinks in monkeys were found to be similar to those found during gaze-evoked blinks in humans. It was found that blinks were more likely to occur during a refixation saccade than a saccade to a target. This was found to occur during both the visually-guided and the memory-guided saccade tasks. This is similar to the results found by Williamson et al. (2005) in head-stabilized humans. They found that humans made fewer blinks when making a saccade to a target than during the returning saccade to the fixation area. Williamson et al. (2005) concluded that this was most likely due to the lower attentional demands during the refixation saccade.
because accuracy was not important. Because of the similar findings in monkeys as in humans, we can postulate that similar mechanisms underlie these observations.

The present study found that larger amplitude saccades were more likely to be associated with a blink in monkeys. Similar results were found by Evinger et al. (1994) in humans. They found that blinks were more likely to occur during gaze shifts that were associated with large movements of the eyes and head.

It was found in this study that saccades in monkeys that were accompanied by a blink were slower than saccades that were not. This is consistent with results found by Goossens and Van Opstal (2000) who also found that the kinematics of a saccade were disturbed by blinks in a similar way. They found that velocity was reduced and that the duration of the saccade associated with a blink was longer than a saccade that was not.

These findings support that common mechanisms underlie gaze-evoked blinks in both humans and rhesus monkeys.

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