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**Different effects of eyelid blinks and target blanking
on saccadic suppression of displacement**

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ABSTRACT

Displacements of visual stimuli during saccadic eye movements are often not noticed. We have demonstrated that this saccadic suppression of image displacement can be eliminated by blanking the stimulus for a short period during and after the saccade (Deubel, Schneider, & Bridgeman, 1996). We here report an experiment in which target visibility was interrupted after the saccade either with distal target blanking or voluntary eyeblink. The data show that the effect of blinking is different from blanking: interruption of vision due to a blink did not enable subjects to detect target displacements any better than they had done in the no-blank condition. The results provide evidence for an extraretinal signal that distinguishes between endogenous and exogenous sources of temporary object disappearance after the saccade.

INTRODUCTION

Saccadic suppression is a reduction of the sensitivity to visual events occurring before, during, and immediately after saccadic eye movements. Two separate types of saccadic suppression should be carefully distinguished. The first type has probably first been described by Dodge in 1898, who noted that words that could be recognized in the periphery during reading pauses could not be seen during saccades. The initial rediscovery of saccadic suppression of image displacement was in a qualitative report by Ditchburn (1955), followed by an independent rediscovery of the effect by Wallach and Lewis (1966). Since then, many studies have investigated the visual sensitivity to short flashes presented around the time of the saccade (for reviews, see Matin, 1974; Ross, Morrone, Goldberg, & Burr, 2001). Typically, these investigations reported a moderate elevation of visual threshold (two to threefold) for detecting spots of light flashed briefly during saccades. Other researchers used more complex visual stimuli such as sine gratings that were briefly presented during saccades. Their results have demonstrated that saccadic suppression is strongest for the low spatial frequencies (below 1 c/deg), while higher spatial frequencies remain largely unaffected (Wolf, Hauske, & Lupp, 1978, 1980; Burr et al., 1994). The selectivity of suppression to the magnocellular pathway strongly suggests that this type of suppression is specific to motion signals (Ross et al., 2001).

The second type of saccadic suppression concerns the strong reduction in sensitivity (by three to four log units) for detecting the spatial displacement of a single target or of the whole visual array, when this displacement occurs shortly before or during a saccade (Bridgeman, Hendry, & Stark, 1975). During fixation, the sensitive motion detectors of the visual system allow to perfectly perceive even very small jumps of visual objects. Due to the high retinal velocity during a saccade, however, these motion signals are basically wiped out with each eye movement. Without direct evidence for a target jump from motion detectors, detection of intrasaccadic image displacement depends on the comparison of the pre- and postsaccadic target locations. The finding that small image displacements are hard to perceive therefore seems to imply either that the required precise comparison is normally not performed, or that transsaccadic memory about the location of objects is not available to the visual system, or is very poor.

However, we have recently provided evidence that a precise memory of presaccadic target location is indeed transferred across the saccade, but that this information is normally not used in displacement detection. In these studies, we demonstrated that blanking a target during a saccade, and presenting it again only 50-300 ms after the saccade end, restores the detectability of even quite small displacements - we called this the “blanking effect” (Deubel & Schneider, 1994; Deubel, Schneider & Bridgeman, 1996; Deubel, Bridgeman, & Schneider, 1998). The blanking effect occurs even for targets in darkness, meaning that displacement detection under this condition can rely on extraretinal signals rather than on retinal information from the structured environment.

Obviously, the considerable accuracy with which subjects can judge transsaccadic displacements in the blanking condition requires both the maintenance of high-quality information about presaccadic target position across the saccade, and a precise extraretinal signal. Thus, it follows from our findings that precise information about the presaccadic target position and a precise extraretinal signal are indeed available for stimulus localizations after the saccade, but they ordinarily are not used in perception. We have suggested that this is because the visual system assumes, as a null-hypothesis, the stability of any object that is continuously available both before and after the saccade. Only a very large discrepancy between eye movement magnitude and image position is able to break this assumption. This assumption is also broken, when the presaccadic object is not present immediately after the saccade. Only under this condition are precise transsaccadic information and extraretinal signals used to achieve displacement detection.

These previous studies investigated spatial and temporal constraints of the effect of an exogenous blanking of the stimulus (Deubel et al., 1996, 1998; Deubel, Schneider, & Bridgeman, 2002). However, there also exists a natural case where visual information is temporarily not available, namely during an eyeblink. Indeed, many large saccades are accompanied by blinks. Using an analog photoelectric method, Stark (1968) showed blinks to obscure the pupil for about 200 ms. Moreover, it has been demonstrated that the onsets of blinks and of (vertical) saccades are very well synchronized (Becker & Fuchs, 1988). Interestingly, the perceptual consequences of blinks are much smaller than the consequences obtained from a similar interruption of visual input during fixation: the blink is perceived as being much shorter than it really is (Volkman, Riggs, & Moore,

1980).

The question arises whether blinks that occur during saccades can induce a blanking effect. A blink extending beyond the end of the saccade induces an endogenous postsaccadic gap in the visual information flow, visually similar to a distal target disappearance. If blinks can function like the blanking intervals demonstrated in our previous research, we would expect subjects to be capable of detecting small jumps of a target during a saccade accompanied by a blink, even if the distal stimulus is continuously present. If the visual system does not process blinks as interruptions of information flow, however, performance should be comparable to that in the no-blank case. Since the retinal information is identical in both conditions, such a finding would imply that non-visual, extraretinal information signals whether the eyes are open, influencing the processing of the postsaccadic target. To study this question, subjects were instructed to perform a voluntary blink during their saccade. The effect of the blink on displacement detection was compared to the effect of an exogenous blanking of the target.

METHODS

Subjects

Four male subjects (aged 26-44) participated in the experiment; one of them was one of the authors of the study (HD). The other three subjects were also members of the laboratory, but they were naïve with respect to the purpose of the experiments. The data of a fifth subject (BB) could not be used in the final analysis since the flash detection experiment (see below) revealed that he did not completely close the eyes during his blinks.

Apparatus

The stimulus consisted of a small red laser dot (diameter 0.2 deg), back-projected via a fast x-y mirror galvanometer system on an opaque screen in total darkness. The laser dot could be switched off and on by means of special purpose hardware within 2 milliseconds. The mirror galvanometers allowed to shift the target by 10 deg within about 3 milliseconds; during the shift, the dot was switched off to prevent a visual streak on the screen. Viewing distance was 1.5 m. Vision was binocular.

Movements of the right eye were recorded with a 2-dimensional search coil based on the principle of Robinson (1963). Three sets of magnetic coils mounted orthogonally in a cubic coil frame (70 cm frame size along an edge) are driven with high-frequency alternating current (20 kHz) in phase quadrature, inducing currents in a small coil embedded in a toroidal contact lens (Skalar Medical, Delft). The lens is held firmly in place on the saddle-shaped surface at the edge of the limbus of the eye. The induced currents are recorded from two fine wires emanating from the search coil. After amplification and phase-locked detection two analog signals are obtained which represent the sine of the horizontal and vertical components of the contact lens orientation. The system is insensitive to head translations within the region of uniform field. It provides a noise level less than 1 min arc peak-to-peak and a linearity error of less than 0.25%.

The analog signals corresponding to horizontal and vertical eye movement were digitized at a frequency of 500 Hz and stored on disk for off-line analysis. A two-point central difference differentiation algorithm (Bahill, Kallman, & Lieberman, 1982) continuously estimated the momentary eye velocity and generated a trigger signal indicating the occurrence of a saccade once the velocity exceeded 15 deg/sec. We verified that the trigger-induced target blanking or target shift consistently occurred in the first third of the duration of the saccade.

Procedure

Two different experimental blocks (“no blink” and “with blink”) were run. Figure 1 displays a typical example for a “no blink” trial in which the solid curve represents the eye movement while the dashed curve shows the target shift and blanking. The subject was instructed to follow an initial step of the laser dot by 6 or 8 deg, to the left or to the right. The onset of the eye movement triggered a saccade-contingent blanking of the target which lasted 0 (no blank), 150, 250, or 400 ms (the case shown in the figure refers to a blanking interval of 150 ms). The target then reappeared at a position displaced 1.3 deg from its original position, either in the same or in the opposite direction of the initial step. At the end of each trial, the subject’s task was to indicate by button press whether the secondary displacement had occurred in the same direction as the initial step or in the opposite direction. The target remained on until the end of the trial; its final position was the starting position for the next trial. In the “no blink” blocks, the subject was instructed

not to blink during the trial. In the “with blink” blocks, the subject was asked to perform a voluntary blink, simultaneously with the saccade. Before data recording began, the subject was given some practice of saccade-contingent blinking with feedback. Each subject performed 3 blocks of each type, each block containing 96 single trials.

<Figure 1 about here>

In the critical experimental condition including the blinks, the recorded eye movement traces were used to analyze the occurrence and the temporal properties of the eyeblinks. This is possible due to the high spatial accuracy of the eye coil signals in which the occurrence of a blink can easily be discriminated from a normal saccade without a blink. The curves in Figure 2 give examples for recorded horizontal and vertical eye position in a trial without blink (left graphs) and a trial including a blink during the saccade (right graphs). It can be seen that the blink typically results in a distinct artifact, particularly clear in the vertical channel. The prominent negative deviation of the vertical eye position signal in the blink case indicates a transient downward component of the eyes which is known to accompany eyeblinks (Collewijn, van der Steen, & Steinman, 1985). Using a specialized custom-made software, we analyzed each blink trial manually to mark the endpoint of the deviation which was taken to indicate the end of the blink (c.f. Figure 2). Since it was difficult to discriminate the start of the blinks from saccade onsets in the traces, we did not mark and analyse blink onsets nor blink durations.

<Figure 2 about here>

An important question was how well these times of the end of the artifact coincided with the onset of vision after each blink. For this purpose, a “flash detection” control experiment was performed in which each trial first started with the laser dot stepping by 6 or 8 deg, to the left or to the right. The laser was blanked after 100 ms. The subject followed the target step with a saccade combined by a voluntary, simultaneous blink. Triggered by the saccade, in 71% of all trials a 5 ms flash of the laser dot was presented at various times during and after the blink, at the target position. In the remaining 29% of all trials, no flash was presented. The subject finally indicated, by pressing one of two buttons, whether he or she had detected the test flash. Each subject performed a total of 280 of these trials.

RESULTS

The result of the “flash detection” control experiment is given in Figure 3, showing the rate of flash detection as a function of the interval between the end of the blink artifact (see Figure 2) and flash occurrence. The vertical bars indicate standard errors. Obviously, the end of the blink-induced artifact in the eye movement traces correlated very well with the onset of vision after the blink. The time at which the individual subjects reached 50% flash detection ranged from 28 to 38 ms before the end of the artifact, yielding a mean of 34 ms. False alarm rate was zero. It is very unlikely that the visibility of the stimulus was effected by saccadic suppression or by blink suppression, since the brightness of the laser spot was far too high. The “flash detection” control experiment thus demonstrates that the times marked in the blink analyses can be used as a quite reliable measure for the onset of visual stimulation after blinks. In order to account for the finding that vision starts, on the average, 34 ms before the end of the artifact, we corrected in the following the end of each blink artifact by this value, finally obtaining an estimate for the time when visual input became available after the blink in each trial.

< Figure 3 about here >

Figure 4 shows percentage of correct discrimination for onward and backward target steps as a function of the blanking period, individually for the four subjects. The data from the „no blink“ blocks are presented as open circles, those from the “with blink” blocks are given as filled circles. The solid vertical line indicates the approximate end of the primary saccade, and the dashed vertical line represents the mean onset time for vision after the blink for each subject as resulting from the analysis of the blink artifact described above.

< Figure 4 about here >

It can be seen that the data of the „no blink“ trials reproduce the blanking effect: Discrimination performance is close to chance for zero blanking, but rises steeply for longer blank durations. For the blocks that include a blink, performance also depends on target blanking. However, now performance improves only with considerably longer blanking durations: the curves are shifted by about 150ms to longer blanking durations, which roughly corresponds to the postsaccadic duration of the blink. A two-way analysis

of variance on the percentage of correct responses, with subjects as replications, showed highly significant effects of the blanking interval, $F(3,9) = 39.9$, $MSe = 28.3$, $p < 0.001$, and of blinking, $F(1,3) = 35.5$, $MSe = 12.2$, $p = 0.009$. The interaction of both variables also reached significance, $F(3,9) = 12.7$, $MSe = 17.7$, $p = 0.001$. Somewhat surprisingly, performance with zero blanking interval was slightly better in the “no blink” as compared to the “with blink” condition ($t(3)=4.7$; $p=0.02$). Possibly, the transients induced by the blink bias the visual system, to some degree, to accept location changes in the visual world across saccades.

Two important implications follow from this data pattern. First, the endogenously induced absence of a stimulus after a saccade due to a blink is interpreted differently from the absence due to a distal target blanking. This can best be illustrated from the difference in performance at a blanking duration of 150 ms which is close to the beginning of viewing at the end of the blink. For both the “no blink” and “with blink” conditions, vision of the target becomes available at about the same time – nevertheless, performance for the exogenous target blanking is far superior to the endogenous, blink-induced blank. Thus the interruption of vision due to the blink did not enable the subjects to do any better than they had done in the no-blank condition. Second, even after the end of a blink, subsequent blanking of the target allows for the detection of its displacement. For all four subjects, performance improves monotonically with longer post-blink blanking intervals.

DISCUSSION

The experiment compared the effects of endogenous eyeblinks and exogenous target blanking on saccadic suppression of displacement. As can be seen from the “flash detection” control experiment, the interruption of vision during a blink is just as complete, and just as long-lasting, as the interruption during many of our blanking experiments (Deubel et al., 1996). Despite this interruption, however, blinks do not elicit a blanking effect -- they do not facilitate detection of differences between presaccadic and postsaccadic target positions. This implies that the space constancy system is informed that an interruption of vision is due to a blink, and does not start to compute postsaccadic target location during the blink if saccade and blink occur simultaneously.

What are the possible sources of information that would allow the visual system to distinguish between exogenous and blink-induced target disappearance? In the natural world, the blink is characterized by a uniform field of low brightness, while an obscured saccade target can be a relatively small feature in a large field of objects and textures. In the laboratory situation of our experiment, however, the retinal consequences of eyeblinks and target blanks are largely identical. A blink is extremely rapid, reaching eyelid velocities of up to 2000 deg/sec during its down-phase and up to 700 deg/sec during its up-phase (Evinger, Manning, & Sibony, 1991). It is primarily the time it takes the lid to transit the central region of the pupil that is important for the detailed time course of the visual transient. Given the high eyelid velocities during a voluntary blink, this time can be estimated to a few milliseconds. In other words, the target disappears and reappears abruptly, with no other change in retinal stimulation. Therefore we have to conclude from our findings that it must be the extraretinal information about the status of the eyeblink system that is used to distinguish between the visual effects of blinking and blanking.

Every time we blink our eyes, the image of the retina goes almost completely dark. Nevertheless, we hardly notice these interruptions, even though a similar external darkening is startling (Volkman, Riggs, & Moore, 1980). Volkman et al. were the first to demonstrate that suppression of flashed visual stimuli occurs not only with saccadic eye movements, but also with eyeblinks. By shining a light through the roof of the mouth of human subjects to permit retinal illumination independent of eyelid position, these authors showed that there is a reduced sensitivity to light around the time of blink onset. This phenomenon has been termed “blink suppression”. In the following, a number of investigators have shown that the suppression of sensitivity around blinks has similar psychophysical properties to the suppression seen in saccadic eye movements, suggesting that the same mechanism might be involved in both cases (e.g., Stevenson, Volkman, Kelly, & Riggs, 1986; Ridder & Tomlinson, 1993, 1995, 1997).

Obviously, different kinds of transients have different perceptual impacts: the sudden change of the retinal image of a scene due to a saccade or a blink does not disrupt the perceptual stability and continuity as much as a similar exogenous change would do. Therefore, in at least some respects the visual system must process different kinds of

transient events differently. Recently, Gawne and Martin (2000, 2002) studied the activity of neurons in various areas of the visual cortex under four different conditions: 1) the stimulus flashing on and off while the eye was fixating; 2) external darkening of the entire scene; 3) stimulus onset and offset induced by a saccade; and 4) offset induced by an eyeblink. The data show that most neurons responded to the on- and offsets in a very similar manner, independent of how the blanking was induced. However, in a substantial minority of cells the response varied strongly as a function of the transient event. So, some neurons in V1 responded with a transient burst of activity to the onset of an external darkening but not to a blink, suggesting that the suppression of this transient causes us to ignore blinks.

The fact that a blink does not act as a blank is probably useful in normal visual perception. Several authors (e.g., Bridgeman, van der Heijden, & Velichkovsky, 1994) have hypothesized that saccadic suppression of image displacement has an important role in preserving perceived stability across saccades - it serves to bridge the errors between extraretinal sources of location information and the actual movement. Deubel et al. (1996) have shown that saccadic suppression of image displacement disappears with a postsaccadic target blanking. Therefore, if the visual system would treat postsaccadic target absence due to a blink just like a distal target blanking, a saccade accompanied with a blink would often result in a perceived instability of the visual world.

In our previous studies we demonstrated that saccadic suppression of image displacement largely disappears when postsaccadic target information is absent immediately after the saccade (Deubel et al., 1996), and that stimuli that are present after the saccade are taken as a spatial reference for localization (Deubel et al., 1998, 2002). This resulted in a new interpretation of the mechanism of transsaccadic space constancy. The finding presented here further specifies properties of the blanking effect and has some theoretical implication as to how visual stability is preserved across saccadic eye movements. According to our theoretical interpretation, visual attention shifts to the saccade target before the saccade is executed (for empirical evidence, see Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996). Due to the attention shift, location and visual attributes of the target and of surrounding objects are stored in transsaccadic memory. Presumably, the capacity of transsaccadic memory is limited to a few, possibly not more than four, visual objects

(Irwin, 1992, 1993). After the saccade, the visual system searches for the previous object of attention within a restricted spatiotemporal „constancy window“ (McConkie & Currie, 1996). The constancy window is about 50 ms in duration, and it is confined to a limited spatial area of a few degrees around the saccade target (Deubel, in press). If the object is found, the world is assumed to be stable. Spatial information from the previous fixation is discarded or ignored, and localization proceeds using the currently available information. The results from the blink experiment suggest that, in the case of eyeblinks, extraretinal information about the eyeblink status is used to inform the space constancy system that the object should not be sought, until the eyes are open.

When, as due to a distal target blanking, the target is not found, the assumption of stationarity of the visual world is broken. Extraretinal signals are used to establish the new target location. Only in this case does the system use stored information about sensory conditions such as target position before the saccade, which results in the detection of intrasaccadic displacements.

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FIGURE CAPTIONS

Figure 1. Target position (dashed curve) and eye position (solid curve) in a trial with stimulus blanking. The target jumped left or right by 6 or 8 deg to elicit a saccade. Triggered by the onset of the saccade, the target was blanked and reappeared after the blanking interval T_B , at a location displaced by 1.3 deg with respect to the previous target position. The subject's assignment was to follow the target, and to report the direction of the second target displacement.

Figure 2. Examples for eye movement traces recorded with the search coil technique in a trial without eyeblink (left plots) and in a trial where the saccade was accompanied by a voluntary eyeblink (right plots). The dashed curves indicate the horizontal target position. Solid curves, upper diagrams: Horizontal eye position. Solid curves, lower diagrams: Vertical eye position. The traces show that the blink leads to a distinct artifact both in the horizontal and in the vertical eye position signal. In order to estimate the time of blink end, the trials were analyzed manually to mark the endpoints of the blink artifacts (vertical dashed-dotted lines).

Figure 3. Control experiment in which the target was flashed for 5 ms, during or after the blink. Data show percentage probability for the detection of the flash as a function of the time between flash presentation and the end of the blink artifact (see Figure 2).

Figure 4. Discriminability of direction of target displacement as a function of blanking interval T_B , for the four subjects. The open symbols show the discrimination performance from trials without eyeblinks. The solid symbols show the data following a combined saccade and blink, plus a varying blanking interval. The solid vertical line in each plot indicates the approximate end of the saccade, and the dashed vertical line displays the mean estimated onset time of vision after the blink for the individual subject.

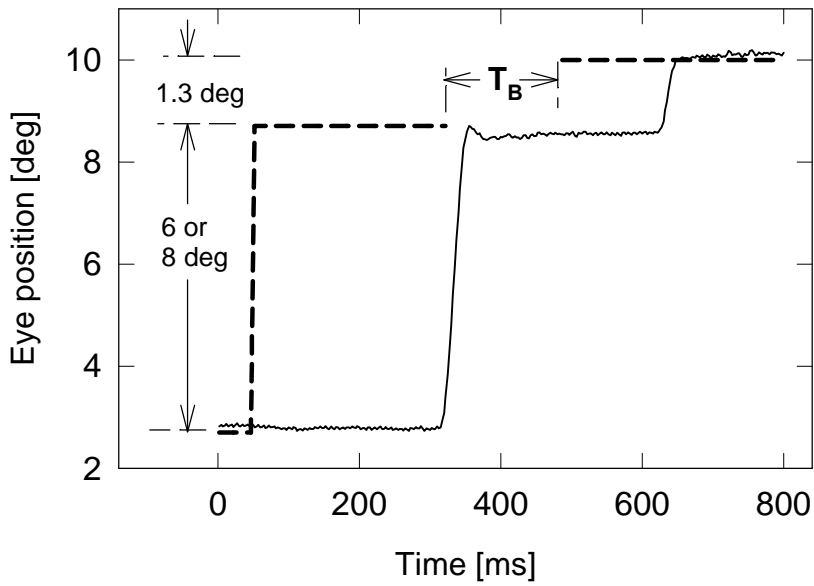


Figure 1

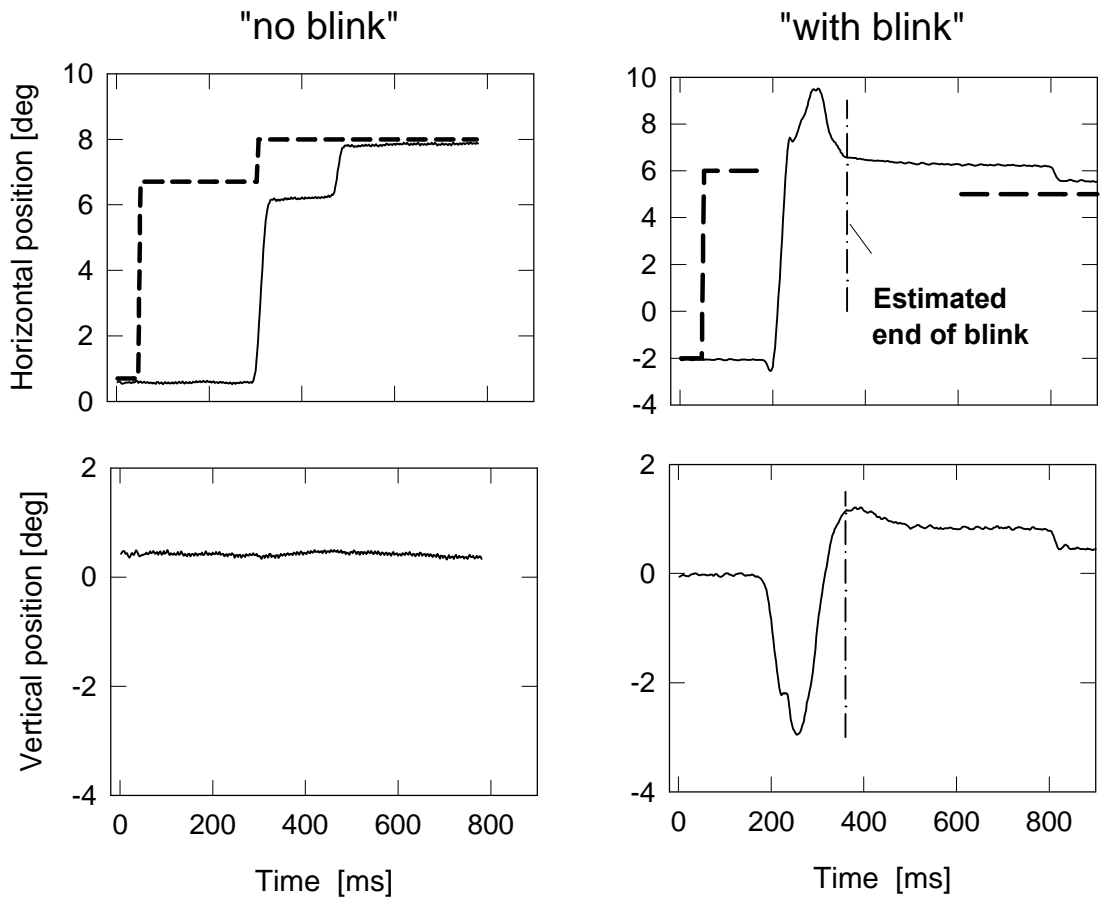


Figure 2

"Flash detection" control experiment

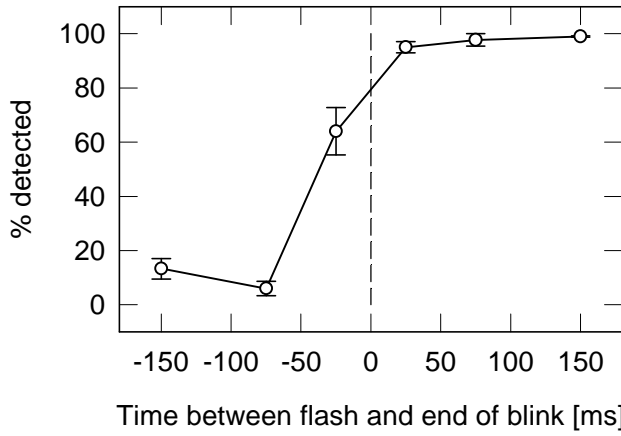


Figure 3

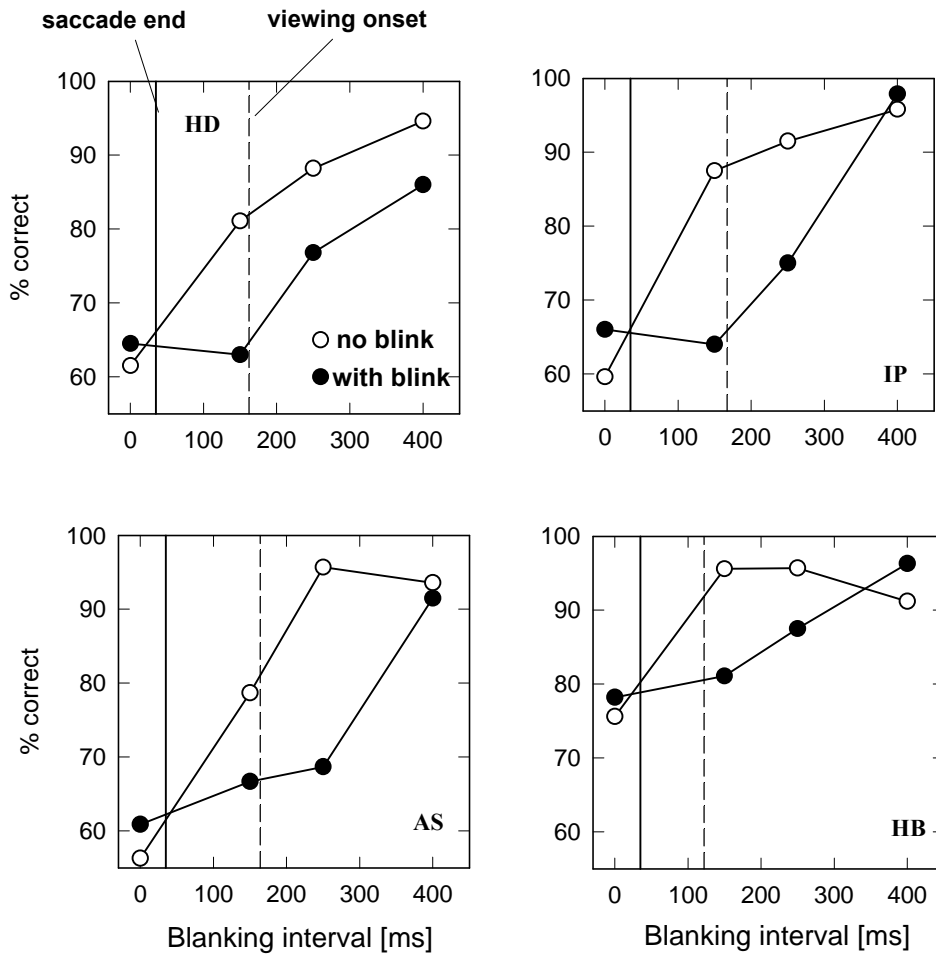


Figure 4