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Perceiving locations of moving objects across eye blinks

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Abstract

Eye blinks cause disruption of visual input that generally goes unnoticed. It is thought that the brain uses active suppression to prevent awareness of the gaps, but it is unclear how suppression would affect the perception of dynamic events, when visual input changes across the blink. Here we addressed this question by studying the perception of moving objects around eye blinks. In Experiment 1 (N = 16), we observed that when motion terminates during a blink, the last perceived position is shifted forward from its actual last position. In Experiment 2 (N = 8), we found that motion trajectories were perceived as more continuous when the object jumped backward during the blink, cancelling a fraction of the space it travelled. This suggests subjective underestimation of blink duration. These results reveal the strategies used by the visual system to compensate for disruptions and maintain perceptual continuity: time elapsed during eye blinks is perceptually compressed and filled with extrapolated information.

Introduction

Humans blink about 20 times per minute, resulting in periods in which the eyelids cover the pupils for more than 100 ms (Lawson, 1948; VanderWerf, Brassinga, Reits, Aramideh, & de Visser, 2003). Yet, these frequent disruptions of the visual input do not lead to disruptions of continuous perception. Instead, we are generally unaware of our own spontaneous blinks. This continuity is thought to rely on inhibitory mechanisms that suppress the conscious visual perception of transients caused by the eyelid closure. Previous psychophysical work showed that light flashes presented through the roof of the mouth, thus bypassing the pupils and eyelids, are suppressed from awareness (Manning, Riggs, & Komenda, 1983; Volkmann, Riggs, & Moore, 1980). Evidence from physiological studies further shows suppression of BOLD activity in response to visual stimuli (Bristow, Haynes, Sylvester, Frith, & Rees, 2005) and of transient activity in early visual cortical areas (Golan et al., 2016).

For static scenes, suppression of these transients may be sufficient to instil a sense of continuity in perception. However, dynamic scenes containing moving objects would require updating of object positions across eye blinks in addition to suppression of the blink-induced transients. The masking or suppression of these transients may itself lead to change blindness, missing small displacements of object positions (Deubel, Bridgeman, & Schneider, 2004; Lau & Maus, 2018; Maus et al., 2017) or larger, otherwise obvious changes to a visual scene across an eye blink (O'Regan, Deubel, Clark, & Rensink, 2000; O'Regan, Rensink, & Clark, 1999). Hence, position changes of objects, stationary *and* moving, may simply be ignored. Another possibility is that the motion of an object is perfectly extrapolated through the duration of the blink, so that the visual system will expect it to reappear at the location consistent with a constant velocity and continuous trajectory.

Motion extrapolation refers to the idea that the visual system uses information from the previous trajectory of a moving object to predict future positions and facilitate processing there (Nijhawan, 2008; Whitney, 2002). At a computational level of description this process has been compared to visual tracking algorithms that combines past inputs with an internal model of motion dynamics to predict where the moving object will go next (Kwon, Tadin, & Knill, 2015). At an implementational level of description the facilitation may be based on a subthreshold spread of neural activity that can speed up processing once actual bottom-up input from these retinal positions is received (Jancke, Erlhagen, Schöner, & Dinse, 2004). It may, however, also lead to a percept of an object in unstimulated positions. In this view, perceiving a moving object typically involves motion extrapolation to compensate for visual processing delays. Strong evidence for the latter hypothesis stems from findings showing that moving objects are perceived in positions without retinal input, e.g. in the retinal blind spot (Maus & Nijhawan, 2008) or the foveal blue scotoma (Shi & Nijhawan, 2012).

It is also possible that in extrapolating an object's movement, the visual system consistently underestimates the distance an object moved during a blink. Support for this notion may come from some recent findings on the perception of time during eye blinks. The duration of visual events occurring around the time of eye blinks seems to be systematically underestimated (Duyck, Collins, & Wexler, 2015; Grossman, Gueta, Pesin, Malach, & Landau, 2019; Irwin & Robinson, 2016). In these experiments, observers judged the duration of visual stimuli that were presented starting before or during a blink and ending afterwards. There was no or only little overestimation of stimulus durations starting during the blink (Duyck et al., 2015; Irwin & Robinson, 2016), which was interpreted as evidence against 'antedating' or 'postdicting' the stimulus onset to the time at the beginning of the blink. This is in contrast to the phenomenon of 'chronostasis', occurring, e.g., in the stopped-clock illusion during saccades, where the onset of a stimulus occurring during the blind phase of the rapid eye movement is antedated to the beginning of the saccade (Yarrow, Haggard, Heal, Brown, & Rothwell, 2001). Stimuli straddling an eye blink were perceived as shorter than the actual duration of the stimulus, control conditions without eye blinks, and auditory stimuli, respectively, by about 117 ms (Irwin & Robinson, 2016), 90 ms (Duyck et al., 2015), or 121 ms (Grossman et al., 2019). This underestimation of elapsed time during an eye blink may in itself support perceptual continuity across blinks, by making the blackout during the blink seem shorter and less salient than it would otherwise appear.

Here we test how the positions of moving objects are perceived across eye blinks. In Experiment 1, we investigate moving objects that disappear during a blink, and ask which position observers will report as the last perceived position, a paradigm similar to classical studies on Representational Momentum (Freyd & Finke, 1984; Thornton & Hubbard, 2002). If observers report a position of the moving object close to where it was when the eyelids closed, that would mean that observers perceive the position accurately. Potentially, since our observers keep their eyes fixated on a stationary stimulus and do not follow the moving object, a small undershoot may be expected (Kerzel, 2000; Maus & Nijhawan, 2009). If observers reported an overshoot beyond the object's position at the time of lid closure, however, this would be evidence for an active extrapolation of the objects position through the eye blink. In this view, since information about the object's disappearance only becomes available to the visual system once the eyelids reopen, the object is continuously extrapolated through the blackout period. Reported final positions of the object close to the expected position at the time of the end of the blink would be evidence for perfect extrapolation through the period of the blink. Intermediate positions would be consistent with incomplete extrapolation through the blink period, or perfect extrapolation but with an underestimation of the blink duration.

In Experiment 2, we further investigated how discontinuities in motion trajectories during blinks are perceived, and whether continuous speed and motion trajectories are assumed for the duration of the blink. While the eyelids were closed during a blink, we introduced a small forward or backward jump of the object, consistent with a temporary speeding up or slowing down of the object. In a 2-alternative forced-choice paradigm, we tested whether observers perceived a forward or backward jump, and whether there was any bias, i.e., whether a trajectory without a jump is indeed perceived as a continuous one, or whether some slowing down or speeding up of the object leads to the most continuous percept. If participants extrapolate the motion of the object perfectly through the duration of the eye blink, no bias in responses would be expected. If they underestimate the duration of their own blink, however, this would predict that backward jumps of the object during a blink are perceived as most continuous.

Experiment 1 – The final perceived position of moving objects disappearing during eye blinks

Methods

Participants

Based on pilot experiments, we expected moderate effect sizes and chose to recruit 16 participants in accordance with similar psychophysical studies in the literature. Optional stopping was not performed.

We recruited a total of 17 volunteers from Nanyang Technological University and paid 10 S$ per hour for their participation. Data from one participant could not be used for the final analysis because of technical issues with the eye tracker, leaving 16 participants (6 female) aged between 19 – 35 years (M = 24.2, SD = 4.8). The study was approved by the Nanyang Technological University Institutional Review Board, and participants provided written informed consent after being briefed about the procedures. All participants had normal or corrected-to-normal vision.

Apparatus and Stimuli

All stimuli were programmed in MATLAB and PsychToolbox extensions (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, & Murray, 2007), and presented on a 21-inch CRT monitor (SUN Microsystems) with a screen resolution of 1152 x 864 at a refresh rate of 100 Hz. Luminance output was linearized using a Minolta LS 1100 photometer. Participants were seated in a dark room at a constant viewing distance of 69.5 cm from the screen, with the use of a chinrest to prevent head movements. Responses were collected via mouse clicks, and eye movements and blinks were recorded with an Eyelink 1000+ eye tracker (SR Research, Ottawa, Ontario) at 1000 Hz sampling rate.

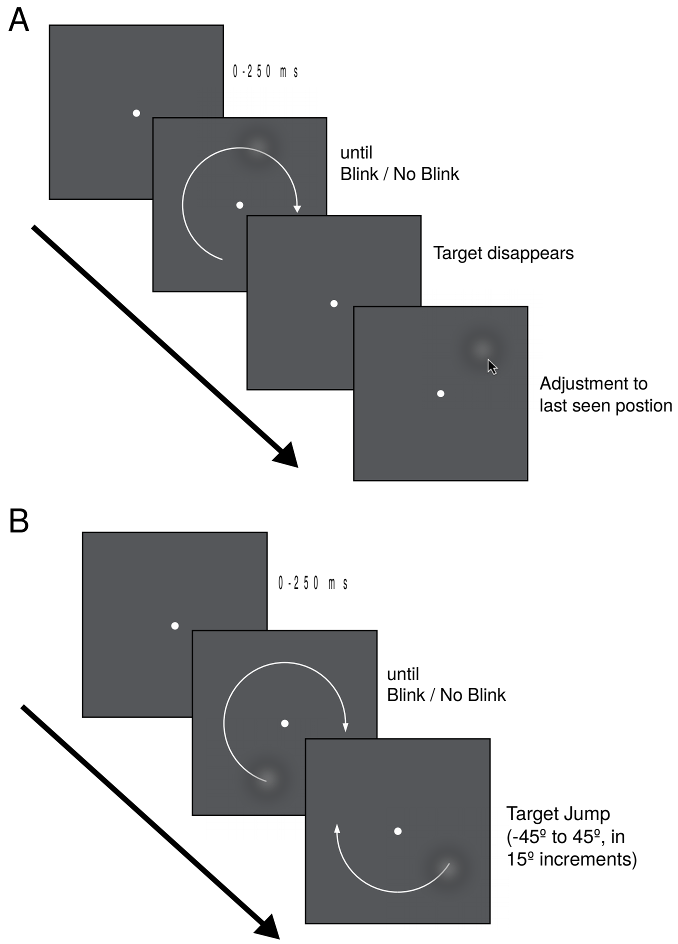

Figure 1. Stimuli of the experiments. A Gaussian blob target was moving on a circular trajectory around the fixation spot (radius = 8º visual angle). **A** In Experiment 1, the target disappeared during a blink (or in a no-blink control condition, at a random time point). Participants had to adjust the target to the last perceived position of the trajectory. **B** In Experiment 2, the target jumped forward or backward during a blink (or at a random time point) and continued moving. After each trial, participants judged whether there had been a forward or a backward jump.

The stimulus used in Experiment 1 consisted of a white Gaussian blob target (maximum luminance: 132 cd/m^2, sigma: 0.15º) travelling on a circular trajectory of 8º radius centred around a white fixation dot (subtending 0.5º visual angle; see Figure 1). The target moved in either a clockwise or counterclockwise direction, at an angular velocity of either 180º/s (slow) or 240 º/s (fast), resulting in tangential velocities of 25.1 or 33.5 degrees visual angle per second, respectively. Direction and speed were selected randomly on every trial within each experimental block. All stimuli were presented on a grey background (66 cd/m^2).

Procedure

Each experimental trial began with a white central fixation dot. Participants were instructed to keep their eyes fixated on the dot throughout the experiment. Successful detection of fixation by the eye tracker on each trial (+/- 2º) was followed by the appearance of the moving Gaussian blob after 0 to 250 ms at a random location on the path of the circular trajectory. Failure to maintain fixation resulted in the trial aborting and returning the display to the fixation screen.

On half of the experimental blocks, participants were instructed to blink while the target was moving (blink condition). Blinks were detected, when the eye tracker's pupil size estimate dropped by more than one quarter from one display frame to the next (within 10 ms), or when the pupil size was zero. Detection of a blink would result in the target disappearing on the next video frame.

On the other half of the experimental blocks, participants were instructed not to blink while the target was moving (no-blink condition). During the no-blink trials, the target would disappear at a random location after a certain period of time based on the average duration until a blink occurred in the previous blink block (jittered by ± 1 *SD*). In both conditions, participants were asked where they perceived the last location of the target to be and responded by using the mouse to move the position of the Gaussian blob cursor to the last perceived location of the moving target and making a mouse click at that location. The radial position error relative to the actual disappearance position at the beginning of the blink was recorded. Responses that were positioned behind the actual final location of the target were termed negative response errors (undershoots), while responses that were ahead of the actual final location of the target were termed positive response errors (overshoots).

Prior to the start of the experimental trials, participants carried out several practice blocks consisting of 40–80 trials of both blink and no-blink conditions to familiarise them with the stimuli and task. Following this, participants completed two blink and two no-blink blocks of 80 experimental trials each in alternating order with a break after the first two blocks. Direction of motion and angular velocity were fully randomized across trials within each block.

Analysis

Response errors on each trial were calculated as the difference in location between the response position and the actual last position of the target on the screen. Note that the target was extinguished on the next monitor refresh frame after the eye tracker lost the pupil signal. In all likelihood, the eyelids are completely closed at this time point. It is even possible that the stimulus is still on screen when the eyes are closed already. Response errors are defined as the difference of the adjusted response position from the last physical position on the screen, and may therefore slightly underestimate the error from the last perceived position. Positive response errors cannot be explained by a misestimation of the moment of eyelid closure, because they correspond to perceiving the stimulus in a position on the screen in which it was never presented.

Trials with blinks in no-blink blocks or without blinks in blink blocks (about 4.1% of trials) were excluded, as were blink durations shorter than 16 ms or exceeding the individual subject's mean blink duration by more than 3 standard deviations (in total 11.1% of trials). Further, trials where the response error was more than ± 3 SD away from the mean were excluded from further analysis (1.3% of trials).

For each participant, we fit a linear regression model of the form

$$\text{ResponseError} \sim N(\mu, \sigma_\varepsilon^2)$$
$$\mu_i = \beta_0 + \beta_1 \cdot \text{Blink}_i + \beta_2 \cdot V_i + \beta_3 \cdot (V_i \cdot \text{Blink}_i) + \beta_4 \cdot (\text{BlinkDuration}_i \cdot \text{Blink}_i)$$

where V_i is a dummy variable that encodes the speed of the stimulus at trial i (0 = 180 °/s, 1 = 240 °/s), Blink_i is another dummy variable that encodes, whether trial i is from a blink (1) or a no-blink (0) block, and β_1, β_2, β_3, β_4 are the linear coefficients. Before performing the regression, each participant's distribution of blink durations (expressed in seconds) was centred, such that the mean was zero. This allows interpreting the main effect of blink condition (the parameter β_1) as the effect of a blink with average duration on response error.

We perform one-sample t-tests on these parameter estimates to evaluate effects at the group level. If not stated otherwise, Bayes factors are computed using the JZS prior (which consists of a Cauchy prior on the standardized effect size and uninformative Jeffreys prior on variances as described by Rouder et al., 2009) and reported to quantify the evidence for the (point) null hypothesis in case of non-significant results. Bayes factors were interpreted according to criteria given by Jeffrey (1961). We preferred to use a default, uninformative prior for the calculation of Bayes factors because our experimental protocol is novel, making it difficult to formulate a specific subjective priors.

Results

To determine if the motion of the target was extrapolated into a blink, and to examine the effect of angular velocity on motion extrapolation, mean response errors of each participant were calculated for each combination of blink × velocity conditions (see Figure 2A). A linear model with motion direction as an additional predictor revealed that direction of motion had no effect on response errors, hence the data was collapsed across directions for all subsequent analyses. We fitted linear regressions to each individual participant (see Methods) and report the group level statistics here. Estimated mean parameters including one-sample t-tests and Bayes factors are shown in Table 1. There was a general overshoot of the perceived final position on blink trials (M = 4.79°, SEM = 1.49), while responses on no-blink trials tended to undershoot the actual last position (M = -1.39°, SEM = .59). The effect of blinks (β_1) was significant, $t(15) = 4.292$, $p = 0.001$; the Bayes factor indicated strong evidence for an effect of blinks on localisation error, BF = 57.9. In Table 1 we report significance tests, Bayes factors and effect sizes for each parameter of the regression model.

Table 1: Means of estimated parameters from GLM fits.

	mean	**SD**	***t*(15)**	***p***	**BF_{10}**	Cohen's d	Cohen's d lower bound	Cohen's d upper bound
β_0 (constant)	-1.22	2.55	1.91	0.076	0.90	-0.48	-0.99	0.04
β_1 (blink)	6.16	5.74	4.29	0.001	57.93	1.07	0.46	1.69
β_2 (velocity)	-0.36	1.28	1.11	0.28	0.33	-0.28	-0.78	0.22
β_3 (blink x velocity)	0.11	2.94	0.14	0.89	0.19	0.04	-0.45	0.53
β_4 (blink duration)	1.20	3.20	1.50	0.15	0.52	0.38	-0.13	0.88

The overshoots during blinks did not scale with speed; angular velocity did not have a significant effect on the magnitude of overshoots. Velocity (β_2) did not reliably predict localisation error, $t(15) = -1.109$, $p = 0.285$; the Bayes factor suggested that the data were 3.0 times more likely under the null hypothesis.

We did not find evidence that trial-by-trial fluctuations of blink duration influenced localization error (parameter β_4), $t(15) = 1.502$, $p = 0.154$; the Bayes factor suggested that the data were 1.93 times more likely under the null hypothesis, indicating that the evidence at the group level did not support conclusively the null hypothesis. In order to get further insight into whether blink durations influence localization errors, we quantified the evidence for the null hypothesis at the level of single subjects. First, we re-estimated the linear regression model for each participant but without including blink-duration as predictor. Next, we calculated the correlation between the residuals of the linear regression and the trial-by-trial values of the blink duration. Finally, we calculated the Bayes factor for the correlation using a default prior developed for testing the nullity of correlations (Ly, Verhagen, & Wagenmakers, 2016). We found that the Bayes factors indicated strong evidence in favor of the null hypothesis ($BF_{01} > 10^{1/2}$) for 13 out of 16 subjects (median BF_{01} 6.18, range from 3.69 to 9.92). For the remaining 3 subjects the Bayes factor did not conclusively support neither the null nor the alternative hypothesis (median BF_{01} 1.11, range from 0.83 to 1.74). In sum, we found that for the majority of our subjects revealed strong evidence that the response error was not modulated by the duration of the blink.

These results indicate that blinks lead to perceived overshoots, when a moving object disappears during a blink. This overshoot, however, does not scale with speed or blink duration. If the disappearance was only perceived in the position the object would have occupied after the blink, the overshoot would be expected to be around 28.53º for slow and 38.04º for fast targets at the median blink duration of 158.5 ms. The overshoots we found were an order of magnitude smaller. Instead of blinks leading to an extrapolation of the object's trajectory until the end of the blink, there seems to be a small, fixed default amount of forward shift of the trajectory's end point. This is nonetheless remarkably different from how abrupt object disappearance is perceived without a blink, which—in general and in this experiment—lead to a small undershoot of the trajectory end point.

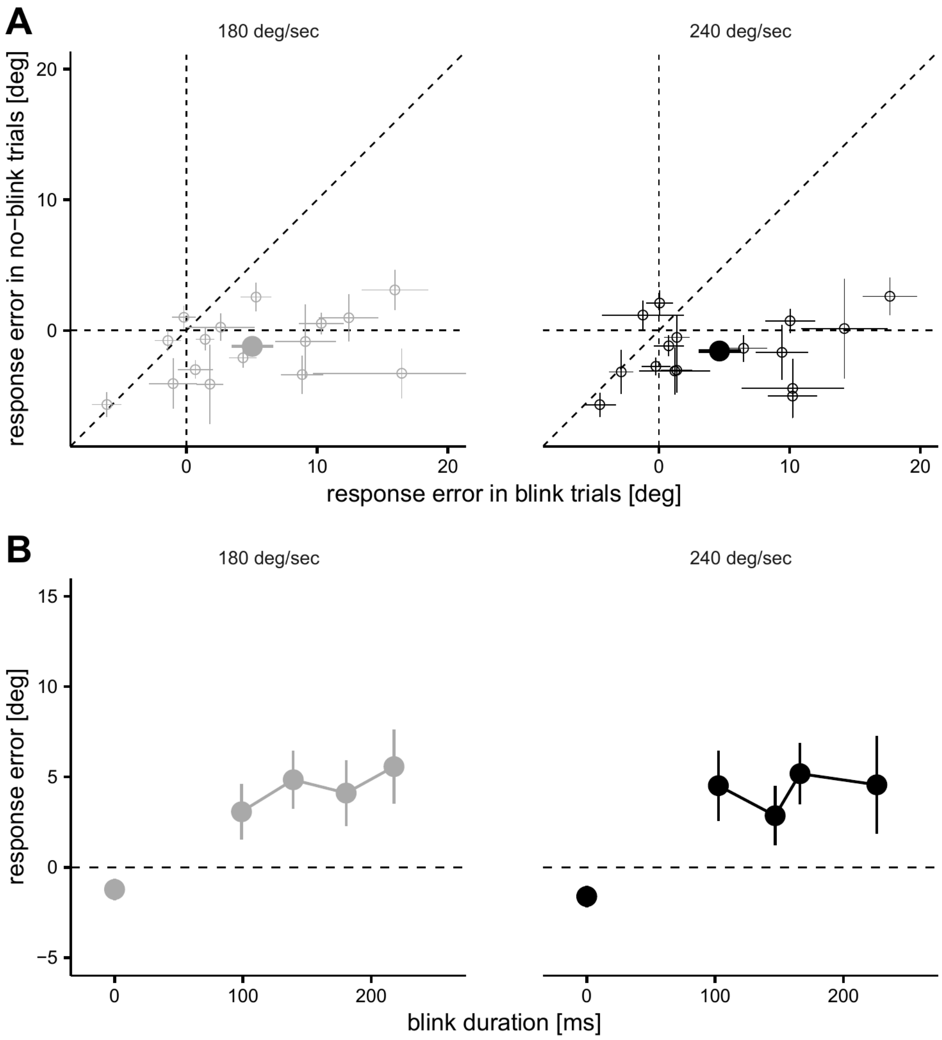

Figure 2. A Response errors (with bootstrapped standard error of the mean) for the adjustment task in Experiment 1. Response error in the no-blink condition is plotted as a function of the response error in the blink condition. Empty dots are individual participants and the filled dots are the group average. Participants saw the target disappear beyond its actual disappearance position when they blinked (overshoot, as indicated by the mostly positive response errors), and perceived a small undershoot without a blink. **B** Mean response errors plotted for blink durations (split in quartiles). The data point at zero shows no-blink trials. There is no apparent relationship of response error and blink duration.

Experiment 2 – Perceiving forward and backward jumps during eye blinks

Methods

Participants

Based on pilot experiments, we expected larger effect sizes than in Experiment 1and chose to test 8 participants. A total of 11 volunteers were recruited from Nanyang Technological University, but data from 3 participants were excluded from the final analysis due to technical issues with the eye tracker, leaving 8 participants (3 male) aged between 22 and 29 years (M = 24.9, SD = 2.6). The study was approved by the Nanyang Technological University Institutional Review Board, and participants provided written informed consent after being briefed about the procedures. All participants had normal or corrected-to-normal vision and were paid 10 S$ per hour for their participation.

Apparatus and Stimuli

The experimental setup and stimuli were similar to Experiment 1. Responses in Experiment 2 were collected via keyboard button presses. The stimulus again consisted of a white Gaussian blob target travelling in a circular trajectory centred on a white fixation dot. The target moved in either a clockwise or counter-clockwise direction, at either slow (180 º/s) or fast (240 º/s) velocities, with direction and speed randomized across trials within each experimental block.

Procedure

Participants were again instructed to fixate on the central dot at all times. Each experimental trial began with a fixation period, and participants were asked to blink once while the target was moving on half of the experimental blocks, and not blink on the other half of blocks. In this experiment the detection of a blink would result in the target jumping either backward or forward on the path of the circular trajectory (Figure 1B). Position jumps ranged in size from -45º to 45º with 15º increments, also including a condition with a 0º jump (i.e., no jump) for a total of 7 possible jump sizes. On the no-blink trials, the target would perform similar jumps after a certain duration of time had elapsed, based on the average duration until a blink occurred in each trial in the previous blink block (± 1 *SD)*. Participants were asked to determine if the target had jumped backward or forward after each stimulus presentation and gave their response by pressing the right or left arrow key to indicate a perceived forward or backward jump.

Prior to the start of the experimental trials, participants carried out several practice blocks consisting of 40–80 trials of both blink and no-blink conditions to familiarise them with the stimuli and task. Following this, participants completed 2 blink and 2 no-blink blocks of 280 experimental trials (7 jump sizes × 2 velocities × 2 directions × 10 repetitions) per block in alternating order with a self-limited break after the first two blocks. All condition combinations of blink, direction, velocity, and jump size were fully randomized across trials.

Analysis

We excluded trials in the same manner as in Experiment 1: Trials with blinks in no-blink blocks or without blinks in blink blocks (2.3% of trials), blink durations shorter than 16 ms (0.15%) and exceeding the individual subject's mean blink duration by more than 3 standard deviations (0.5% of trials) were excluded.

For each participant, we fitted a Generalized Linear Model (GLM) with a probit link function, equivalent to cumulative Gaussian psychometric curves, of the form

$$\Phi^{-1}\,[p(\text{forward})_i] = \beta_0 + \beta_1 \cdot \text{Blink}_i + \beta_2 \cdot \text{JumpSize}_i + \beta_3 \cdot \text{V}_i \\ + \beta_4 \cdot (\text{JumpSize}_i \cdot \text{Blink}_i) + \beta_5 \cdot (\text{V}_i \cdot \text{Blink}_i) \\ + \beta_6 \cdot (\text{JumpSize}_i \cdot \text{V}_i) + \beta_7 \cdot (\text{Blink}_i \cdot \text{BlinkDuration}_i) \\ + \beta_8 \cdot (\text{Blink}_i \cdot \text{JumpSize}_i \cdot \text{V}_i)$$

where Blink_i is a dummy variable encoding the presence of a blink, V_i encodes the speed of the stimulus at trial i (0 = 180 º/s, 1 = 240 º/s), and JumpSize_i represents the size and direction of the abrupt jump of the moving object at trial i. Before performing the regression, each participant's distribution of blink durations was centred, such that the mean was zero. This allows interpreting the main effect of blink condition (the parameter β_1) as the effect of a blink with average duration on the probability of responding "forward" jump. Parameters $\beta_{1\text{-}8}$ are then estimated for each participant using maximum likelihood estimation. Note that although the model is formulated as GLM, the parameters can be directly mapped to those of the psychometric function as shown in the following simplified example:

$$p(y_i) = \Phi\left(\frac{x_i - \mu}{\sigma}\right)$$

$$\Phi\left(\frac{-\mu}{\sigma} + \frac{1}{\sigma} x_i\right)$$

$$\Phi(\beta_0 + \beta_1 x_i)$$

$$\mu = \frac{-\beta_0}{\beta_1}, \sigma = \frac{1}{\beta_1}$$

Thus, we computed the points of subjective equivalence (PSEs) of each condition for each subject. This represents the jump size which the participant is equally likely to report as a forward or a backward jump. We run a 2x2 repeated-measures ANOVA on these values with the condition (blink vs. no blink) and velocity as predictors. As mentioned above, these values correspond to the value of PSEs expected for a blink with average duration: we calculated the slope of the PSEs to blink duration, $\frac{\Delta PSE}{\Delta BlinkDuration}$, separately for each velocity, and ran t-tests on the slopes to test whether blink duration had any systematic effect on the PSE.

Results

Responses from individual participants are shown in Figure 3A. PSEs were determined by fitting probit GLM separately for each participant. Before computing PSEs, we verified that the frequency of "forward" responses was modulated by jump size by performing for each observer a likelihood ratio test between the full model (see Analysis subsection above) and a reduced model that assumed that the frequency be independent of jump size. The test was significant for each participant (all $p < 10^{-9}$). The individual and mean PSEs are shown in Figure 3B. The PSEs for jump sizes during blinks were shifted in the backward direction by 9.2º (SEM = 2.9º) for slow-moving targets and 27.0º (SEM = 6.7º) for fast-moving targets (Figure 3B), whereas PSEs for no-blink trials were shifted backward by 3.7º (SEM = 2.3º) and 7.7º (SEM = 1.9º) for slow and fast targets, respectively. The results of the ANOVA for PSEs revealed that there was a significant main effect of blink, $F(1, 7) = 14.05$, $p = .0072$, $\eta_p^2 = 0.80$ and a significant main effect of angular velocity, $F(1, 7) = 10.09$, $p = .0156$, $\eta_p^2 = 0.66$. The interaction for blink × angular velocity was not found to be significant, $F(1, 7) = 5.21$, $p = .0565$, $\eta_p^2 = 0.43$, however, there is a trend for faster motion to lead to a larger effect. The results revealed that the PSE for target jumps during blinks was shifted toward backward jumps, i.e., participants perceived backward jumps of the moving object as more continuous. No-blink trials also showed a small PSE shift.

Having established that PSEs are shifted toward backward values in the blink conditions, next we assessed whether they were also influenced by trial-by-trial fluctuations in blink duration. For each participant, we calculated the expected rate of change in PSE due to the deviation of blink duration from the individual mean, measured in seconds. The average slope across participants was -38 º/sec (SD 117 º/sec), which was not significantly different from zero, $t(7)=0.93$, $p=0.38$, $BF_{01}=2.66$. The Bayes factor indicate that the data are about 2.7 times more likely under the null hypothesis that participants' judgments were not modulated by trial-by-trial blink duration, which is considered inconclusive evidence. Similar to Experiment 1, we further investigated the evidence for the null hypothesis at the single subject level. However, since there is no default prior for probit GLM, we refit the models using a Bayesian approach. All parameters were given broad, weakly regularizing prior (Normal distributions with mean zero and standard deviation of 10). The prior for the parameter coding for the effect of trial-by-trial blink duration was given as a prior a Normal distribution with mean zero and standard deviation given by the speed of the stimulus averaged across conditions (210º/sec), divided by the scale (parameter σ) of each participant as estimated in blink trials. This corresponds to setting a Normal prior on $\frac{\Delta PSE}{\Delta BlinkDuration}$ with mean zero and the average speed (210º/sec) as standard deviation. The models were fit using MCMC sampling in Stan (Stan Development Team, 2018). The estimated values of the slope $\frac{\Delta PSE}{\Delta BlinkDuration}$ obtained from the Bayesian model were virtually identical to those obtained from the frequentist maximum likelihood fit (correlation $r \cong 1.00$, $p < 10^{-12}$). For each participant, we calculated the Bayes factor using the Savage-Dickey density ration method. We found that the Bayes factors indicated strong evidence in favor of the null hypothesis for 3 out of 8 subjects (median BF_{01} 4.78, range from 4.63 to 8.91). For another 3 subjects the Bayes factor did not conclusively support neither the null nor the alternative hypothesis (median BF_{01} 1.21, range from 0.37 to 2.34). The last two subjects showed instead strong evidence against the null (their values of BF_{01} were 0.206 and 0.001). Thus, in the case of judgments about stimuli that do not disappear during the eye blink we found quite clear individual differences: while few participants clearly did take into account their blink durations, other seemed to not do so and extrapolate the target position only by a default, fixed duration.

Judgements during blink trials were more varied and difficult, with psychometric functions showing flatter slopes. A 2x2 repeated-measures ANOVA on slope values revealed a significant main effect of blink, $F(1, 7) = 10.62$, $p = .014$, $\eta_p^2 = 0.94$, and no evidence for an effect of velocity, $F(1, 7) = 0.00$, $p = .98$, $\eta_p^2 = 0.00$, nor an interaction between blink and angular velocity, $F(1, 7) = .70$, $p = .43$, $\eta_p^2 = 0.09$.

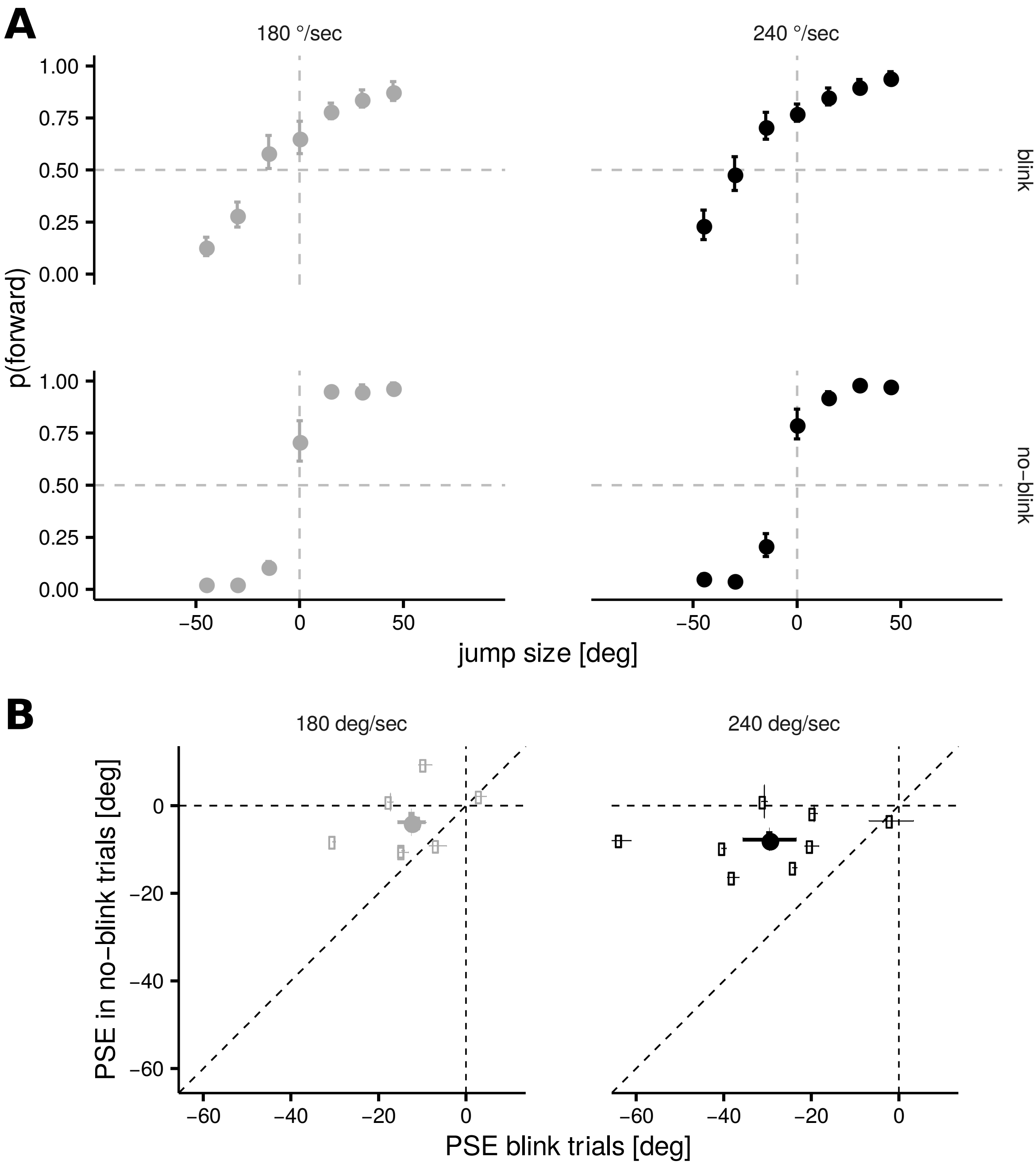

Figure 3. A Mean responses across subjects for jump sizes (dots with bootstrapped standard errors) and individual psychometric functions for all 8 participants. **B** Individual PSEs (open symbols) and means (filled symbols) in blink trials and no blink trials for slow (left) and fast motion (right).

These findings are generally consistent with an underestimation of the distance that the object should have moved during the blink. This shortening of the expected trajectory during the blink could be due to an underestimation of speed during the blink, or due to an underestimation of the duration of the blink. The spatial effect scales with the speed of motion and translates to an underestimation of the time that elapsed during the blink by about 69 to 123 ms (for slow- and fast-moving targets, respectively). The underestimation does not seem to take into account the precise length of the blink for all participants, though, since different blink durations did not significantly impact the misestimation of the target's trajectory. Some participants, however, showed evidence for taking into account the precise blink duration.

Discussion

In this study, we investigated how eye blinks influence the perception of moving objects. Eye blinks interrupt the visual input, but typically do not disrupt the perception of continuous dynamic events in the external world. To maintain continuous perception, a moving object's trajectory might be extrapolated through the duration of a blink.

In Experiment 1, we found that an object disappearing during a blink is indeed perceived to disappear in a position beyond its final retinal position—a perceptual overshoot. The final perceived position was in retinally unstimulated areas, in positions that the object would have occupied only after the eyelids were closed. In contrast, control conditions, in which the object disappeared while the eyes remained open, led to a mislocalization of the perceived disappearance point in the opposite direction of motion—a perceptual undershoot, consistent with earlier findings (Kerzel, 2000; Maus & Nijhawan, 2009).

Nonetheless, the final perceived position with blinks is still short of the position that the object would have occupied when the eyes reopen, had it continued moving. This implies that the object's motion is not extrapolated perfectly through the blink, as might be expected, because the first evidence for the object's disappearance enters the visual system only after the end of the blink. A less then complete extrapolation of the object's motion might be expected, if velocity of the object during the occlusion by the eyelid is underestimated (Palmer & Kellman, 2002), or if the duration of the blink is underestimated by the visual system, as is suggested by some recent findings (Duyck et al., 2015; Grossman et al., 2019; Irwin & Robinson, 2016). In that case we would expect a forward shift of the moving object equivalent to the perceived duration of the blink and consistently scaled by the object's velocity. However, in Experiment 1, the position of the object seemed to be shifted forward by a constant amount in spatial terms (a fixed distance), rather than in temporal terms (a fixed time), since it did not scale with the speed of motion. This result may appear surprising, since other motion-induced forward shifts of perceived positions, such as the flash-lag effect, typically scale with velocity (Nijhawan, 1994; 2008). However, it is consistent with studies that investigated the magnitude of these effects at the termination of an object movement and found no dependence on speed (Kanai, Sheth, & Shimojo, 2004). These results suggest that observers can use information about the extent of spatial extrapolation applied to moving objects, which usually increases with speed, to improve the localization of motion offsets. According to this idea the effect of the eye blink during motion offsets would be to reveal part of the extrapolation by increasing both the temporal and spatial uncertainty about the physical endpoint.

In Experiment 2, we tested whether continuous motion with constant speed during an eye blink is perceived as most continuous, or whether speeding up or slowing down of the moving object is required to perceive continuous motion. To this end, participants judged whether they perceived a forward or a backward jump in an otherwise continuous trajectory, when forward or backward jumps of various sizes were introduced during an eye blink.

We found a bias to perceive backward jumps (or a slowing down of the moving object) as most continuous. PSEs of psychometric function fits were shifted towards backward jumps and scaled with velocity. This bias is consistent with the notion that the visual system underestimates the time elapsed during the blink. If the subjective duration of the blink is shorter than the actual duration, but the object is perceived to move continuously at constant speed, then a shorter distance traveled during the blink should be perceived as most continuous. The PSE shift was larger for faster speeds of motion, but did not seem to scale consistently with blink duration for all participants. This means that the mechanism causing the underestimation of elapsed time during the blink may not compensate for the exact blink duration. Instead, our results imply that duration is underestimated by a constant value between about 70-120 ms.

This range is consistent with previous findings on perceptual compression of blink durations (Duyck et al., 2015; Grossman et al., 2019; Irwin & Robinson, 2016), and is approximately equal to typical average blink durations. There is no evidence for a correlation of underestimation of elapsed time during a blink with individual blink durations, neither from our study nor earlier results in the literature. The subjective underestimation may be based on a 'corollary discharge' or 'efference copy'—a copy of the blink motor plan—with no access to up-to-date measures of an individual blink's duration. Experiments manipulating blink durations, e.g., by comparing reflexive, spontaneous, and voluntary eye blinks, may provide further evidence on whether the visual system uses a default blink duration in all cases, or whether it may update blink duration estimates based on recent empirical measures.

Differently from Experiment 1, in Experiment 2 we observed that the shift in PSE was modulated by the speed of the moving object. As mentioned above, this difference might reflect the special status of the motion endpoints, which are usually not mislocalized, versus points in the middle of the motion trajectory. Indeed, contrary to Experiment 1 where accurate localization would require the cancellation of any extrapolation applied to the moving object, in Experiment 2 accurate judgments would require perfect extrapolation. Taken together our results thus demonstrate the limits of visual perception across eye blinks, by revealing that predictive processes normally engaged in tracking moving objects' positions, can neither be ignored when they are unnecessary for the task (as shown in Experiment 1), nor do they allow a perfect filling-in of gaps in visual input caused by eye blinks (as shown in Experiment 2). In particular, Experiment 2 suggested that the filling-in of gaps in visual input is incomplete due to the compression of the eye blink duration to a stereotypical interval that underestimates the physical duration and, for the majority of participants in our study, does not faithfully take into account trial-by-trial variation in blink duration.

Experiment 2 also showed that the ability to judge forward and backward jumps during blinks is inferior to judgements while the eyes are open. Psychometric functions for the blink condition are shallower than for the control condition with eyes open, indicating greater uncertainty. This is consistent with the suppression of displacement of target positions during blinks that has previously been reported for stationary targets (Deubel et al., 2004; Maus et al., 2017). Additionally, the visual system may assume strong correlations of object velocities over time, and thus perceive smooth, rather than jerky, trajectories with higher probabilities (Kwon, Tadin, & Knill, 2015). Under high uncertainty induced by blinks, the system would rely more on these prior assumptions and discontinuities should be suppressed or ignored. This may explain why the effect reported here does not generally lead to perceiving forward jumps of moving objects, when we blink in daily life. However, in laboratory conditions, such as in the experiments reported here, perception of these jumps can indeed be quantified.

Conclusions

Our findings add to recently renewed interest in perception around the time of eye blinks. For example, observers show a dilation of time in a period following seconds after a spontaneous blink, a finding thought to be related to striatal dopamine expressed by blinks (Terhune, Sullivan, & Simola, 2016). Direct psychophysical measures of perceived durations during a blink showed a compression of elapsed time (Duyck et al., 2015; Grossman et al., 2019; Irwin & Robinson, 2016). The findings by Grossman and colleagues (2019) show time compression specific to judgments of durations of visual stimuli; an auditory stimulus was not similarly compressed, mirroring analogous findings on time compression around saccades (Morrone, Ross, & Burr, 2005). Here we used judgements of positions of moving objects as a more indirect measure of time perception. Nonetheless, we found striking biases in localization of moving objects (Experiment 1) and judgments of continuity of motion (Experiment 2) that are presumably caused by a perceptual compression of time during blinks, indicating that the perceived compression is by no means an isolated phenomenon, but can influence perception of other features such as motion attributes.

Author Contributions

M. Lisi and G.W. Maus developed the study concept. All authors contributed to the study design, the data analysis and interpretation. Testing and data collection were performed by H.L. Goh. G.W. Maus drafted the manuscript, and H.L. Goh and M. Lisi provided critical revisions. All authors approved the final version of the manuscript for submission.

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