Report

Current Biology

Target Displacements during Eye Blinks Trigger Automatic Recalibration of Gaze Direction

Highlights

- Displacements of a visual target during eye blinks can go unnoticed
- Eye movements nevertheless anticipate these unseen target displacements
- Visual signals recalibrate eye gaze position across eye blinks

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In Brief

When a visual target is moved during an eye blink, this can go unnoticed. Maus et al. report that repeated target displacements during eye blinks are nevertheless corrected by automatic eye movements. This points to a recalibration mechanism that adjusts eye gaze to ensure visual stability across blinks.

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Report

Target Displacements during Eye Blinks Trigger Automatic Recalibration of Gaze Direction

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SUMMARY

Eye blinks cause disruptions to visual input and are accompanied by rotations of the eyeball [1]. Like every motor action, these eye movements are subject to noise and introduce instabilities in gaze direction across blinks [2]. Accumulating errors across repeated blinks would be debilitating for visual performance. Here, we show that the oculomotor system constantly recalibrates gaze direction during blinks to counteract gaze instability. Observers were instructed to fixate a visual target while gaze direction was recorded and blinks were detected in real time. With every spontaneous blink—while eyelids were closed—the target was displaced laterally by 0.5° (or 1.0°). Most observers reported being unaware of displacements during blinks. After adapting for ~35 blinks, gaze positions after blinks showed significant biases toward the new target position. Automatic eye movements accompanied each blink, and an aftereffect persisted for a few blinks after target displacements were eliminated. No adaptive gaze shift occurred when blinks were simulated with shutter glasses at random time points or actively triggered by observers, or when target displacements were masked by a distracting stimulus. Visual signals during blinks are suppressed by inhibitory mechanisms [3–6], so that small changes across blinks are generally not noticed [7, 8]. Additionally, target displacements during blinks can trigger automatic gaze recalibration, similar to the well-known saccadic adaptation effect [9–11]. This novel mechanism might be specific to the maintenance of gaze direction across blinks or might depend on a more general oculomotor recalibration mechanism adapting gaze position during intrinsically generated disruptions to visual input.

RESULTS

Humans blink between 5 and 20 times per minute. Eye blinks last for between 40 and 200 ms, during which the eyelids completely cover the pupils and no focused image is present on the retina. Despite this drastic disruption to the visual input, we do not generally notice our own blinks. We definitely do not perceive the world to transiently disappear every time we blink. Retinal responses during eye blinks are suppressed by the visual system [3–6, 12], as demonstrated, for example, in experiments that stimulated the retina via high-intensity light flashes through the roof of the mouth to bypass the occlusion of the pupil by the eyelid [3]. This active suppression of the retinal transients associated with lid closure and opening reduces the disruption of visual input, although other mechanisms may play a role in reducing the apparent duration of the interruption [13].

In addition to the temporal disruption, each eye blink is associated with an involuntary eye movement. Generally, the eyeballs move downward and nasally and return close to their original position from before the blink [1]. This eye movement is due not to mechanical forces of the eyelid on the orbit but to an active neural signal [14, 15]. Like every motor action, this eye movement is subject to noise [2, 16]. Retinal position displacements introduced by blink-induced gaze shifts are generally not perceived as illusory object motion. In fact, small artificial displacements of a visual target during an eye blink go unnoticed [7, 17], and even large changes to the contents of a visual scene are often not detected [8]. This suppression of displacements during blinks might be a consequence of the suppression of visual signals mentioned above. However, any systematic retargeting errors over repeated eye blinks would lead to accumulating errors that are potentially debilitating for perception and the interaction with the environment. How then does the oculomotor system minimize these errors and ensure that, on average, the retina ends up in the same position after a blink?

Here, we investigate whether systematic retargeting errors during spontaneous eye blinks can drive an adaptive retargeting of gaze based on the differences in the retinal image before and after the blink. To do so, we systematically manipulated the position of a fixation target during repeated eye blinks without the knowledge of the observer. We found that the oculomotor system adapts to repeated target displacements during blinks

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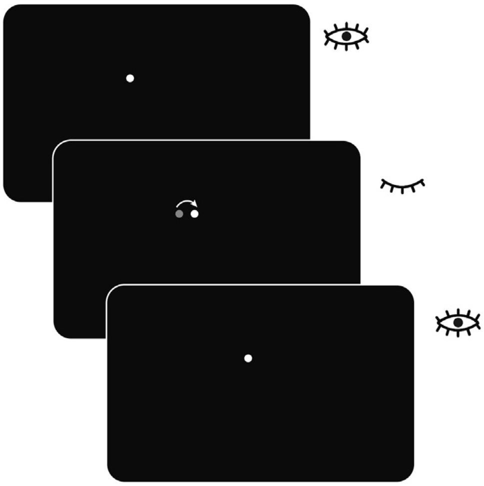

Figure 1. Experimental Stimuli

Participants fixated a single white dot projected on a screen in a dark room. An eye tracker recorded gaze position, and eye blinks were detected in real time. Every time a blink was detected during the adaptation phase, the dot jumped 0.5° to the right (or 1.0° in separate sessions) while the eyelid was closed. We analyzed the first eye gaze position after the blink until the first saccade. In experiments 2–4, we simulated blinks using shutter glasses, and the dot jumped while the shutter glasses were closed.

so that subsequent blinks are accompanied by an eye movement that anticipates the displacement of the target by bringing its expected post-blink position into the center of gaze.

In experiment 1, observers adapted to a consistent target step to the right during each eye blink. Separate sessions employed target steps of 0.5° or 1.0° visual angle, respectively. The experiment started with a baseline phase consisting of 10 blinks without a target step, followed by the adaptation phase with consistent target steps during each blink, lasting for 60 blinks (Figure 1). After the adaptation phase, there were 10 blinks without a target step to assess potential aftereffects. This was followed by three cycles of top-up adaptation with 15 blinks with target steps and 5 blinks without (see Supplemental Experimental Procedures). Random jumps not coinciding with blinks made sure that the target remained in the central region of the screen throughout the experiment, despite cumulative jumps during blinks to the right. We assessed how the introduction of repeated target steps influenced the horizontal gaze position after each blink. We analyzed the gaze position after blinks by averaging the horizontal gaze signal from the time eye tracker noise due to partial occlusion of the pupil subsided up to the first saccade after the blink (or a maximum duration of 200 ms). Figure 2 shows one observer's gaze position traces around the time of a blink from baseline, early and late adaptation phases, and from the first blink without a target step after adaptation. Note that the gaze position after the blink is initially maintained close to the same spatial location as before the blink, subject to some motor noise (Figure 2A). However, after several blinks with a consistent step of the fixation target to the right, the post-blink gaze is eventually corrected to the shifted location (Figures 2B and 2C). This shift is maintained for a few blinks when the stimulus shift is no longer applied (Figure 2D). Figure 3A shows averaged post-blink gaze positions for five observers from each phase of the experiment: baseline, early adaptation (first 10 adaptation blinks), late adaptation (last 10 adaptation blinks), and the first blink after adaptation (aftereffect).

A two-way repeated-measures ANOVA showed significant main effects for step size ($F(1,3) = 13.38$, $p = 0.0216$) and phase of the experiment ($F(3,12) = 31.45$, $p < 10^{-5}$). During the baseline phase, the post-blink gaze position on average showed no significant bias for any particular direction (small step: mean = −0.068°, SEM = 0.070°, one-sample t test: $t(4) = -0.9740$, two-tailed $p = 0.3852$; large step: mean = 0.116°, SEM = 0.038°, $t(4) = 3.13$, $p = 0.0351$; Bonferroni-corrected α for eight comparisons: $\alpha = 0.0063$). In the early adaptation phase (first 10 blinks with a target step), post-blink gaze position was also not significantly biased (small step: mean = 0.116°, SEM = 0.136°, $t(4) = 0.8491$, $p = 0.3046$; large step: mean = 0.272°, SEM = 0.055°, $t(4) = 4.98$, $p = 0.0076$), although a trend might already be apparent. Figure S1A shows the development of bias during the adaptation phase. In the late adaptation phase, gaze positions after the blink were significantly biased toward the target position (small target step: $t(4)$ 14.29, $p = 0.0001$; large target step: $t(4) = 7.59$, $p = 0.0016$). For small target steps of 0.5°, this bias amounted to 0.349° (SEM = 0.024°); for large steps, the bias was 0.614° (0.081°). In both cases, the adaptation compensated for on average ~60%–70% of the target step.

The gaze position after the first blink in the aftereffect phase (when the target no longer stepped during the blink) was similarly biased in the direction of the expected displacement of the target, as in the late adaptation phase (small step: mean = 0.278°, SEM = 0.042°; large step: mean = 0.663°, SEM = 0.058°), exhibiting a significant gaze aftereffect (small step: $t(4) = 6.60$, $p = 0.0027$; large step: $t(4) = 11.53$, $p = 0.0003$). Aftereffects, however, subsided quickly (Figure S1B). Gaze position after the second blink in the aftereffect phase showed a statistically significant bias for the large step only (small step: $t(4) = 1.78$, $p = 0.1499$; large step: $t(4) = 5.43$, $p = 0.0056$, Bonferroni-corrected α for five comparisons: $\alpha = 0.01$). By the third blink after adaptation, there were no more significant biases (small step: $t(4) = 4.50$, $p = 0.0108$; large step: $t(4) = 4.28$, $p = 0.0128$), although a small trend might persist even five blinks after adaptation.

Naive observers did not report noticing the target jumps during each blink. Even the co-authors taking part in the experiment reported not being able to detect the small target step when it coincided with a blink, although perception was not explicitly probed in this experiment.

Simulated Eye Blinks Do Not Lead to Adaptation

Is the observed adaptation of gaze direction in experiment 1 due to eye blinks, or does it also occur for other disruptions of the visual input? To evaluate this possibility, we conducted experiment 2, where we repeated the procedure with simulated blinks using shutter glasses, through which eye movements and pupil size could still be monitored when the shutters were open. To simulate eye blinks, we closed the shutter glasses at random time intervals based on the same observers' natural blink behavior in experiment 1 (Figure S2). Mean gaze positions after simulated blinks are shown in Figures 3B and S1C. From the figures, it is readily apparent that no adaptation of gaze occurred. An ANOVA revealed no significant main effects or interactions,

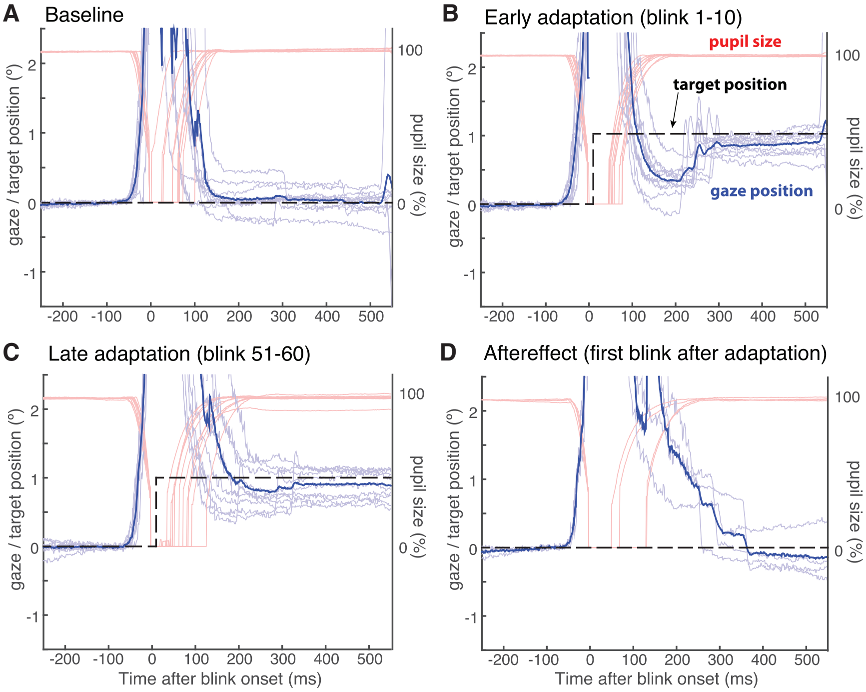

Figure 2. Gaze Position Traces from One Observer in Experiment 1, 1° Target Step

The plots show horizontal gaze positions (faint blue lines), as well as pupil size (faint red, normalized to the pupil size before blink onset) around the time of an eye blink. Gaze position estimates are not available when the eyelid is closed and faulty when the pupil is partially covered. Dark blue lines show average gaze positions for ten blinks (four blinks in D), dashed black lines show target positions. See also Figures S2 and S3.

(A) Baseline phase of the experiment without target steps. Gaze positions after the blink are close to the original gaze position but subject to noise on individual blinks.

(B) Early adaptation phase. Note that the target step occurs while the eyelid is closed (pupil size = 0%). Gaze directions are already biased toward the new target position. Saccades recenter the fixation target on the fovea.

(C) In the late adaptation phase, gaze positions after the blink are strongly biased toward the target position. Correcting saccades are sometimes not necessary.

(D) The first blinks with no target step after adaptation show a strong aftereffect. Gaze direction after the blink is biased toward the expected target position; a correcting saccade occurs in the opposite direction.

and none of the post-blink gaze positions in any phase of the experiment differed from the pre-blink gaze position (all $|t|(2) < 5.73$, $p > 0.0291$, Bonferroni-corrected α for eight comparisons $\alpha = 0.0063$).

Apart from the lack of adaptation, the perceptual experience of these simulated blinks was markedly different. All observers reported detecting the target steps without difficulty and perceiving clear apparent motion of the target, consistent with earlier findings that “blanks” do not cause similar suppression of displacement as blinks [7].

The differences in gaze behavior between experiments 1 and 2 might occur because voluntarily executed eye blinks afford some temporal “warning signal” to the oculomotor system that could be used to facilitate the recalibration. To evaluate whether the null result of experiment 2 was due to the lack of anticipation for the simulated blink, we presented a 300-Hz sine wave tone 200 ms before each closure of the shutter glasses in experiment 3. Results for the eye gaze after simulated blinks are shown in Figures 3C and S1D (see also Figures S3A–S3D). Again, no systematic changes in gaze position after adaptation occurred. An ANOVA revealed no significant main effects or interactions, and none of the gaze positions in any phase of the experiment differed from the gaze position before the simulated blink (all $|t|(4) < 1.92$, $p > 0.1504$).

It is possible that the effects in experiment 1 occur because of observers’ voluntary decision to blink, whereas in experiments 2 and 3, simulated blinks occurred at random time points not under control of observers. In experiment 4, we investigated whether simulated blinks (i.e., closures of the shutter glasses) that are voluntarily triggered by observers via a button press can lead to similar adaptation of gaze as with eye blinks in experiment 1. Mean gaze positions for this experiment are shown in Figures 3D and S1E. Although it might appear as if the late adaptation phase produced a bias, especially for the large target step, this trend is mostly driven by one participant’s noisy data. ANOVA and t tests revealed no significant effects (all $|t|(4) < 3.53$, $p > 0.0242$, Bonferroni-corrected α for eight comparisons $\alpha = 0.0063$).

The conditions involving shutter glasses produced no evidence for adaptive retargeting of gaze, but observers did report seeing clear apparent motion of the target, whereas in the blink conditions observers rarely did. Are blinks necessary for the adaptive eye movement to occur, or can another stimulus that masks perception of the apparent motion also lead to similar adaptation? To test this, we masked the step of the fixation target by displaying a field of random dots for 200 ms in experiment 5. This mask-stimulus made it hard for naive observers to detect the target steps, similar to “mudsplash”-induced change blindness [18]. Results for this experiment mirrored those for the experiments with shutter glasses (Figures 3E and S1F): no corrective eye movement occurred before the target was displayed in the new position, and post-mudsplash eye positions did not differ from positions before the mudsplash (all $|t|(4) < 2.21$, $p > 0.0925$).

Finally, in experiment 6, we asked whether the adaptation could be due to saccadic eye movements occurring during the blinks. We induced blink adaptation as before and then tested whether adaptation transferred to a sequence of saccades similar to blink-related eye movements—downward and nasally in the right eye and back to the target. Because eye movements during blinks are disconjugate and saccades are conjugate, the direction of the eye movement was matched for the right eye only. No transfer of adaptation occurred, and neither did adaptation to a target step during a saccade sequence transfer to

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subsequent blinks (Figures S3E and S3F; Supplemental Experimental Procedures).

DISCUSSION

In summary, repeated displacements of a fixation target during eye blinks lead to automatic eye movements to the anticipated target position during subsequent blinks. The recalibration of eye gaze after blinks develops quickly. Trends for a bias of gaze position toward the anticipated target can be seen after only a few blinks with inducing target steps and reach plateau after around 35 blinks. Aftereffects are short-lived and subsided by the third blink without a target step. The recalibration of gaze only occurs for real eye blinks. Simulated blinks did not lead to anticipatory eye movements to the target position, even when they were temporally cued or actively triggered by the observer. Perceptually, displacements during simulated blinks were clearly visible as apparent motion, whereas displacements during blinks were hardly detectable [7, 17]. Some perceptual effects of saccades, such as spatial compression and suppression of displacement, also occur for visual masks [19, 20]. Perceptually masking the apparent motion of the target using a distractor stimulus, however, was not sufficient to induce the adaptation effect. Real eye blinks are necessary, indicating that in addition to the visual changes before and after the blink, an oculomotor signal is required to trigger this form of gaze adaptation.

Our results for gaze adaptation during blinks mirror many properties of saccadic adaptation. When saccades consistently land short of or overshoot their target due to intra-saccadic target displacements, motor errors are adaptively counteracted by decreasing or increasing the amplitudes of subsequent saccades [9–11, 21]. Saccadic adaptation compensates for about the same proportion of target displacements as "blink adaptation" (gains of 60%–70%) [22–24]. In addition, displacements during saccades are hard to detect [25], matching the observations here for blinks. However, it is important to note that while blinks are often accompanied by saccades [26], involuntary eye movements during blinks are not identical to saccades. They are disconjugate, instead of conjugate [26–28], do not follow the "main sequence" relationship of amplitude and velocity [28, 29], and do not include a pause or fixation period before moving back. Patient studies have shown dissociations between saccades performed with or without accompanying

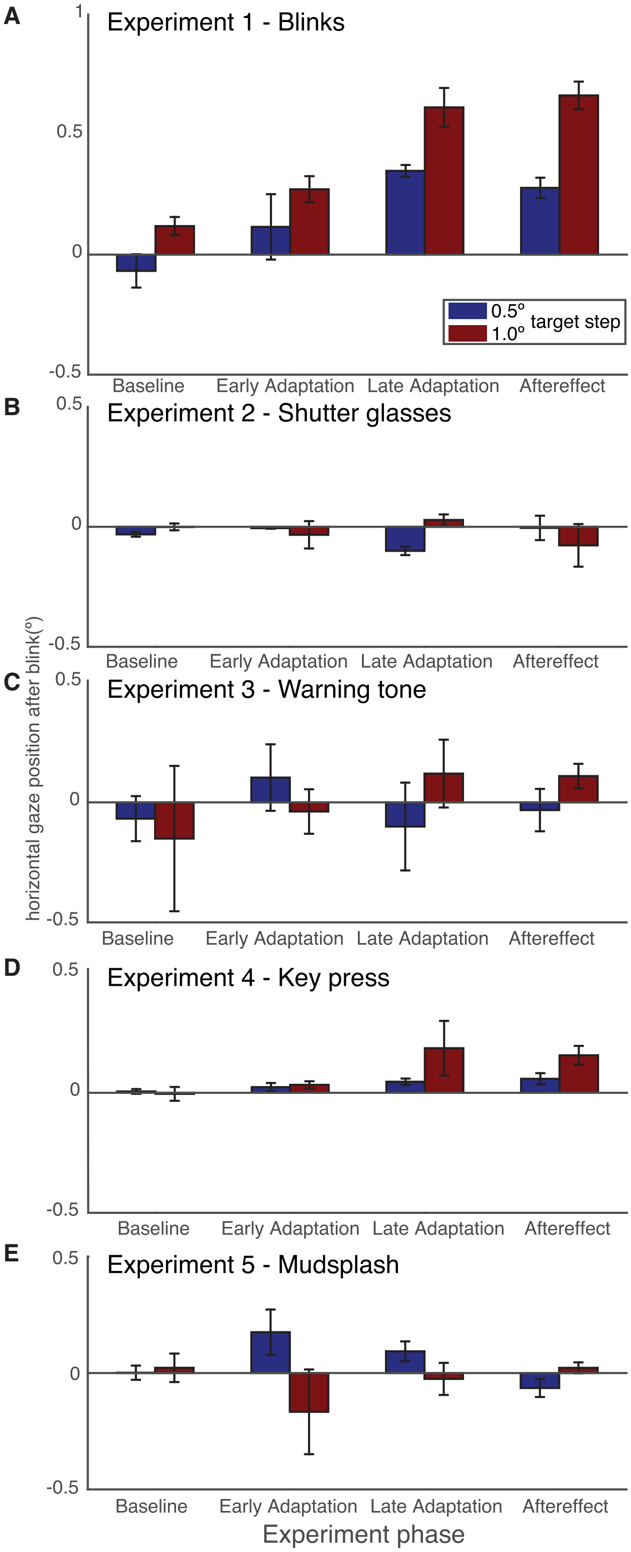

Figure 3. Mean Post-blink Gaze Positions for Different Phases during Each Experiment

The post-blink gaze positions are averaged from the time eye tracker noise due to partial occlusion of the pupil subsides up until the first saccade after a blink (Supplemental Experimental Procedures). Error bars represent SEM. The leftmost bars show the baseline before the target step was introduced (10 blinks). Early adaptation is the mean of the first 10 adaptation blinks, and late adaptation is the last 10 adaptation blinks (blinks 51–60). The rightmost bars (aftereffect) show the mean of the first blink without a target step after the long adaptation and each top-up adaptation (average of 4 blinks per observer). See also Figures S1 and S3.

(A) Experiment 1: observers (n = 5) adapted to a 0.5° target step (blue) or a 1.0° target step (red) during real blinks.

(B) Experiment 2 (n = 3): simulated eye blinks using shutter glasses.

(C) Experiment 3 (n = 6): simulated blinks with warning tones before each closure of the shutter glasses.

(D) Experiment 4 (n = 5): simulated blinks triggered voluntarily by observers via key presses.

(E) Experiment 5 (n = 5): presentation of a random-dot mudsplash mask instead of (simulated) blinks.

blinks [30, 31]. Furthermore, blink adaptation did not transfer to a sequence of a downward and an upward saccade that roughly matched the size and direction of blink-related eye movements, nor did adaptation to a target step during such a saccade sequence transfer to subsequent blinks. Therefore, the adaptation effect reported here is not just an instance of saccadic adaptation. Despite similarities, our results indicate that an adaptive recalibration of gaze can also be triggered by blinks.

The nature of the eye movement achieving this recalibration remains an issue for investigation. Microsaccades occurring after a blink have been shown to partially correct for blink-induced gaze instability [2], but the adaptive eye movement reported here is anticipatory and occurs during the blink. In a recent study, Khazali et al. [16] showed that one function of blink-related eye movements is to reset the torsional position of the eye. They also reported that small blink-induced instabilities in horizontal and vertical gaze position were corrected by this novel type of eye movement. The anticipatory recalibration of gaze reported here might be achieved by adapting the same type of blink-related eye movements themselves [1, 16].

Alternatively, an involuntary anticipatory saccade might be executed coinciding with each blink [27, 28, 32]. In either case, our results raise the intriguing possibility that a general mechanism for the active recalibration of the oculomotor system is triggered by any self-induced disruption of visual processing, such as those caused by saccades, but also by blinks.

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.12.029.

AUTHOR CONTRIBUTIONS

Conceptualization, G.W.M, M.D., M.L., T.C., D.W., and P.C.; Software, G.W.M. and M.L.; Formal Analysis, G.W.M.; Investigation, G.W.M. and M.D.; Writing – Original Draft, G.W.M.; Writing – Review & Editing, G.W.M, M.D., M.L., T.C., D.W., and P.C.; Funding Acquisition, D.W. and P.C.

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