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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 eye ball [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 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 towards 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 the 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 focussed 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 eye balls move downward and nasally and return close to their original position from before the blink [1]. This eye movement is not due to mechanical forces of the eyelid on the orbit, but due 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, 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 3 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 analysed 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 (Fig. 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 (Fig. 2B and C). This shift is maintained for a few blinks when the stimulus shift is no longer applied (Fig. 2D). Figure 3A shows averaged post-blink gaze positions for 5 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).

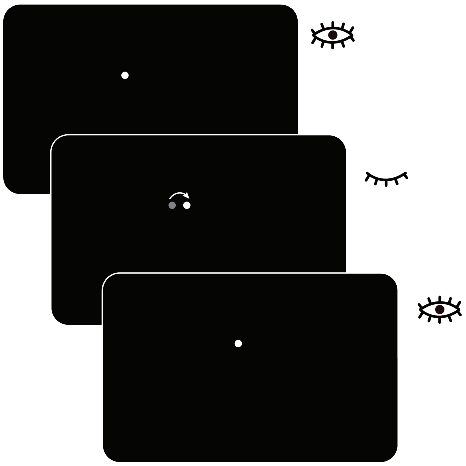

Figure 1. Experimental stimuli
Participants fixated a single white dot projected on a screen in a dark room. An eye tracker recorded gaze position and eye blinks were detected in real-time. Every time a blink was detected during the adaptation phase, the dot jumped 0.5° to the right (or 1.0° in separate sessions) while the eyelid was closed. We analysed 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.

A 2-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°, S.E.M. = 0.070°, one sample t-test: t(4) = -0.9740, two-tailed p = 0.3852; large step: mean = 0.116°, S.E.M. = 0.038°, t(4) = 3.13, p = 0.0351; Bonferroni-corrected α for 8 comparisons: α = 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°, S.E.M. = 0.136°, t(4) = 0.8491, p = 0.3046; large step: mean = 0.272°, S.E.M. = 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 towards 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° (S.E.M. = 0.024°); for large steps the bias was 0.614° (0.081°). In both cases the adaptation compensated for on average about 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°, S.E.M. = 0.042°; large step: mean = 0.663°, S.E.M. = 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 5 comparisons: α = 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 5 blinks after adaptation.

Naïve 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 behaviour in Experiment 1 (Figure S2). Mean gaze positions after simulated blinks are shown in Figure 3B (and S1C). From the figure it is readily apparent that no adaptation of gaze occurred. An ANOVA revealed no significant main effects or interactions, 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 8 comparisons α = 0.0063).

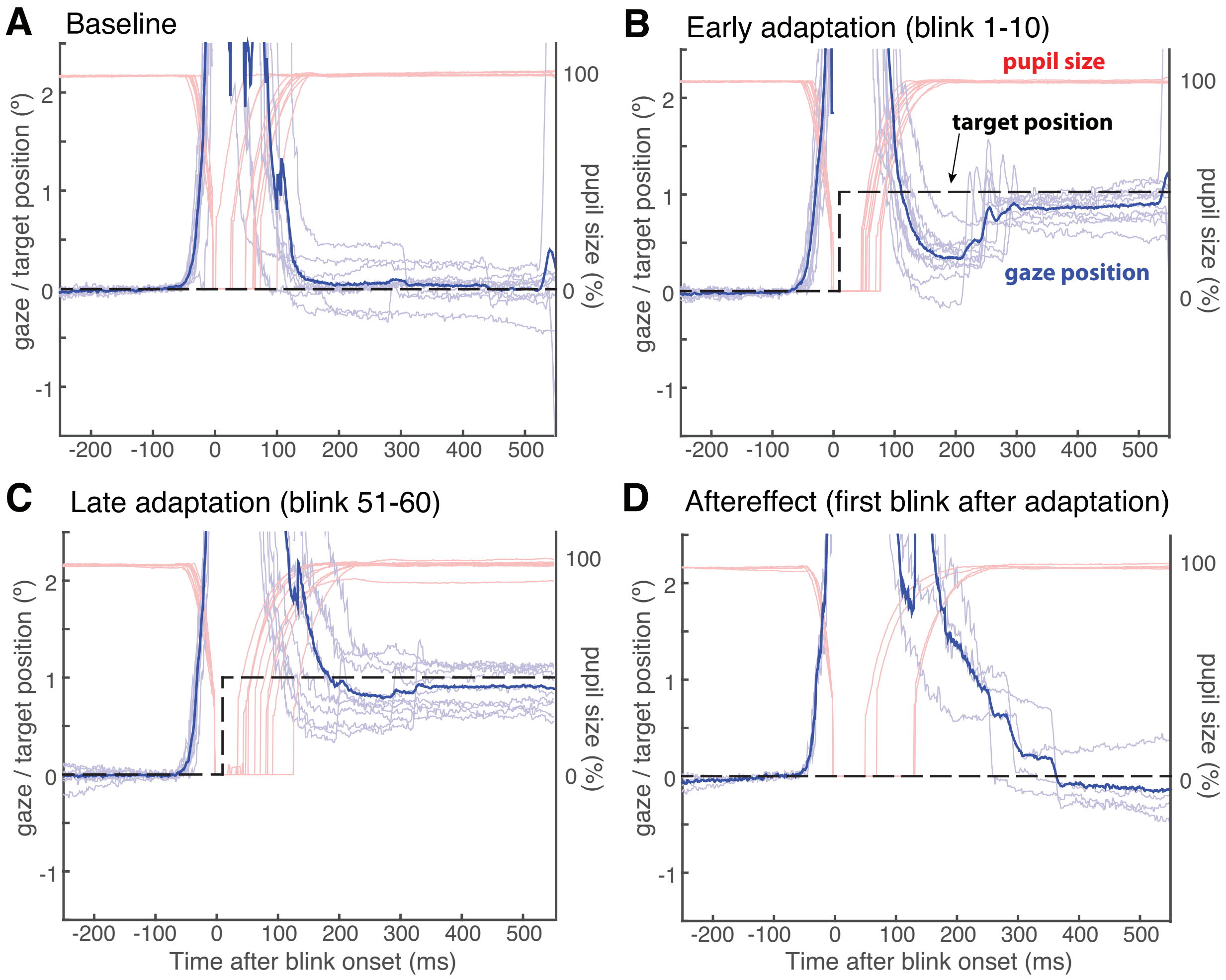

Figure 2. Gaze position traces from one observer in Experiment 1 (1° target step)
The plots show horizontal gaze positions (faint blue lines), as well as pupil size (faint red, normalized to the pupil size before blink onset) around the time of an eye blink. Gaze position estimates are not available when the eyelid is closed and faulty when the pupil is partially covered. Dark blue lines show average gaze positions for 10 blinks (4 blinks in panel D), dashed black lines show target positions. **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 towards the new target position. Saccades re-center the fixation target on the fovea. **C** In the late adaptation phase, gaze positions after the blink are strongly biased towards 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 towards the expected target position; a correcting saccade occurs in the opposite direction. Also see Figures S2 and S3.

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].

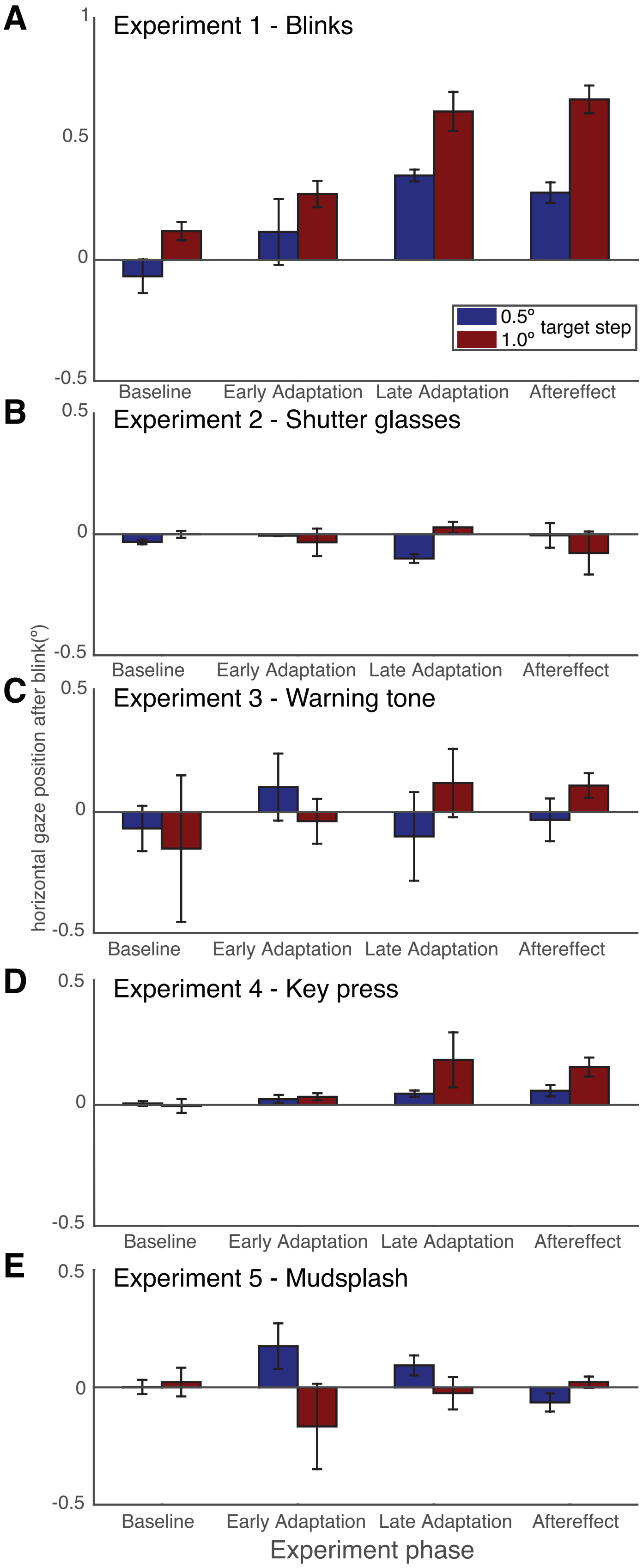

Figure 3. Mean post-blink gaze positions for different phases during each experiment

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 standard errors of the mean. 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, *Late Adaptation* the last 10 adaptation blinks (blink #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). **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. Also see Figures S1 and S3.

The differences in gaze behaviour 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 Figure 3C (and Figure S1D, also see Figure S3A-D). 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 Figure 3D (and Figure 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 8 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 naïve 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 (Figure 3E and S1F): no corrective eye movement occurred before the target was displayed in the new position; 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 subsequent blinks (Figure S3E-F and 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 towards 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 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.

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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Supplemental Figures

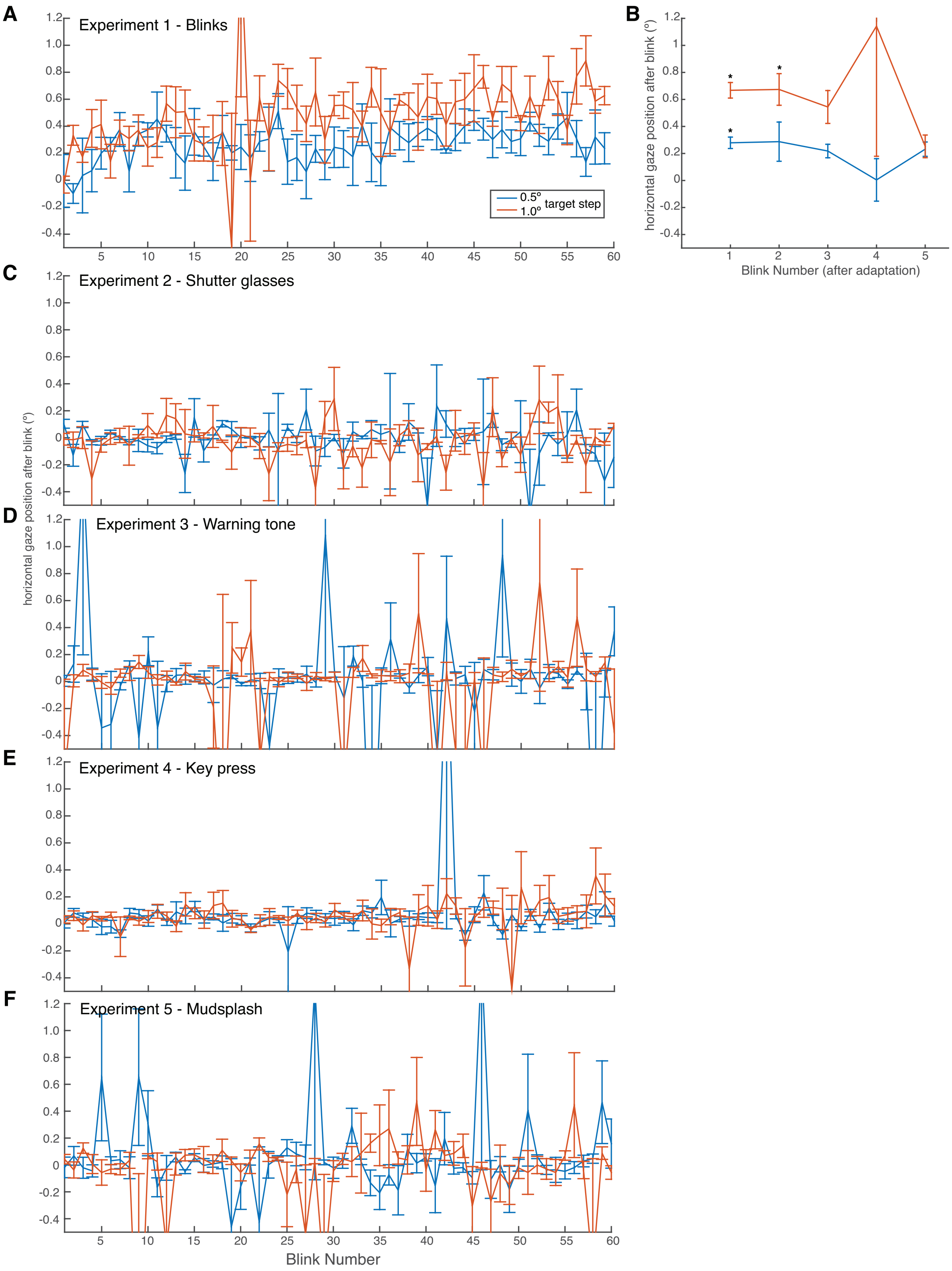

Figure S1. Related to Figure 3. Time course of adaptation in Experiments 1-4. The plots show the mean post-blink gaze direction after each blink (or simulated blink) for all observers. Error bars indicate standard errors of the mean. **A** Adaptation to real blinks in Experiment 1 (n = 5). The post-blink gaze position is biased towards more rightward positions (positive numbers) even after only short adaptation, and seems to asymptote after about 35 blinks. Note that large target steps of 1.0° (red) lead to larger gaze position biases than small target steps (blue). **B** The mean post-blink gaze direction for blinks without target displacements after the adaptation phases in Experiment 1. Asterixes indicate significant one-sample t-tests (with Bonferroni-corrected $\alpha = 0.01$). The first blink without a target step shows a significant bias towards the anticipated target position, similar to the late adaptation phase (panel A). By the third blink, the aftereffect is no longer significantly different from zero (although some small bias may linger until the fifth blink after adaptation). The remaining panels show adaptation to **C** simulated blinks with shutter glasses in Experiment 2 (n = 3), **D** simulated blinks preceded by a warning tone in Experiment 3 (n = 5), **E** simulated blinks triggered by the observer in Experiment 4 (n = 6), and **F** a “mudsplash” mask of random dots instead of blinks or shutter glasses in Experiment 5. Experiments 2-5 did not exhibit systematic biases in post-blink gaze position, and no systematic differences between small and large target steps. Noisy data, (e.g., in Experiments 3) result from when one subject made a large saccade coinciding with the closure of the shutter glasses, or re-fixated on one of the random dots in Experiment 5.

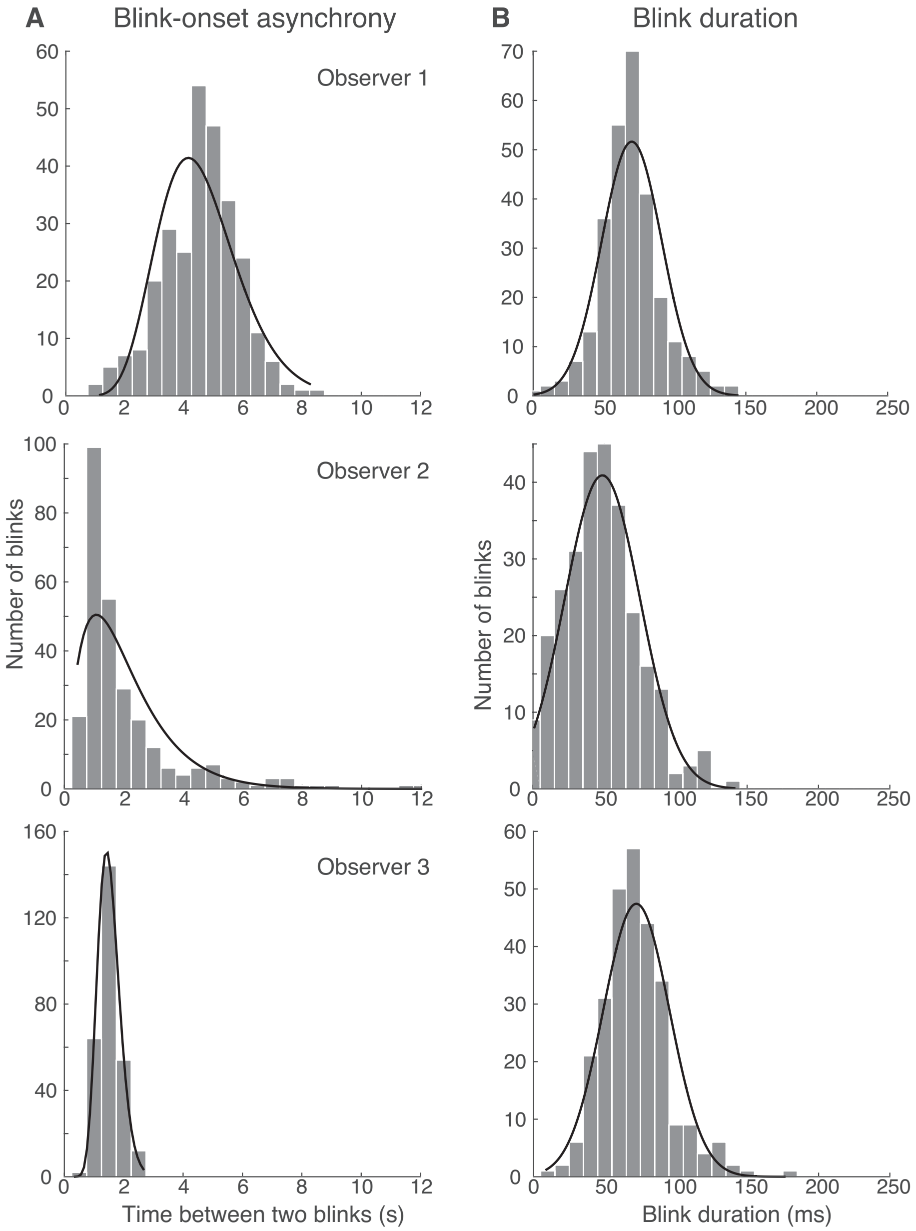

Figure S2. Related to Figure 2. Histograms of blink-onset asynchronies and blink durations.

Different observers in Experiment 1 showed different distributions of blink-onset asynchronies and blink durations (3 observers shown here). **A** Histograms for the time between two successive blinks in the experiment. The black lines are fitted gamma distributions that were used to generate a sequence of random times for simulated blinks in Experiments 2 and 3. **B** Histograms for blink durations. The black lines are fitted normal distributions that were used to generate durations for simulated blinks in Experiments 2-4.

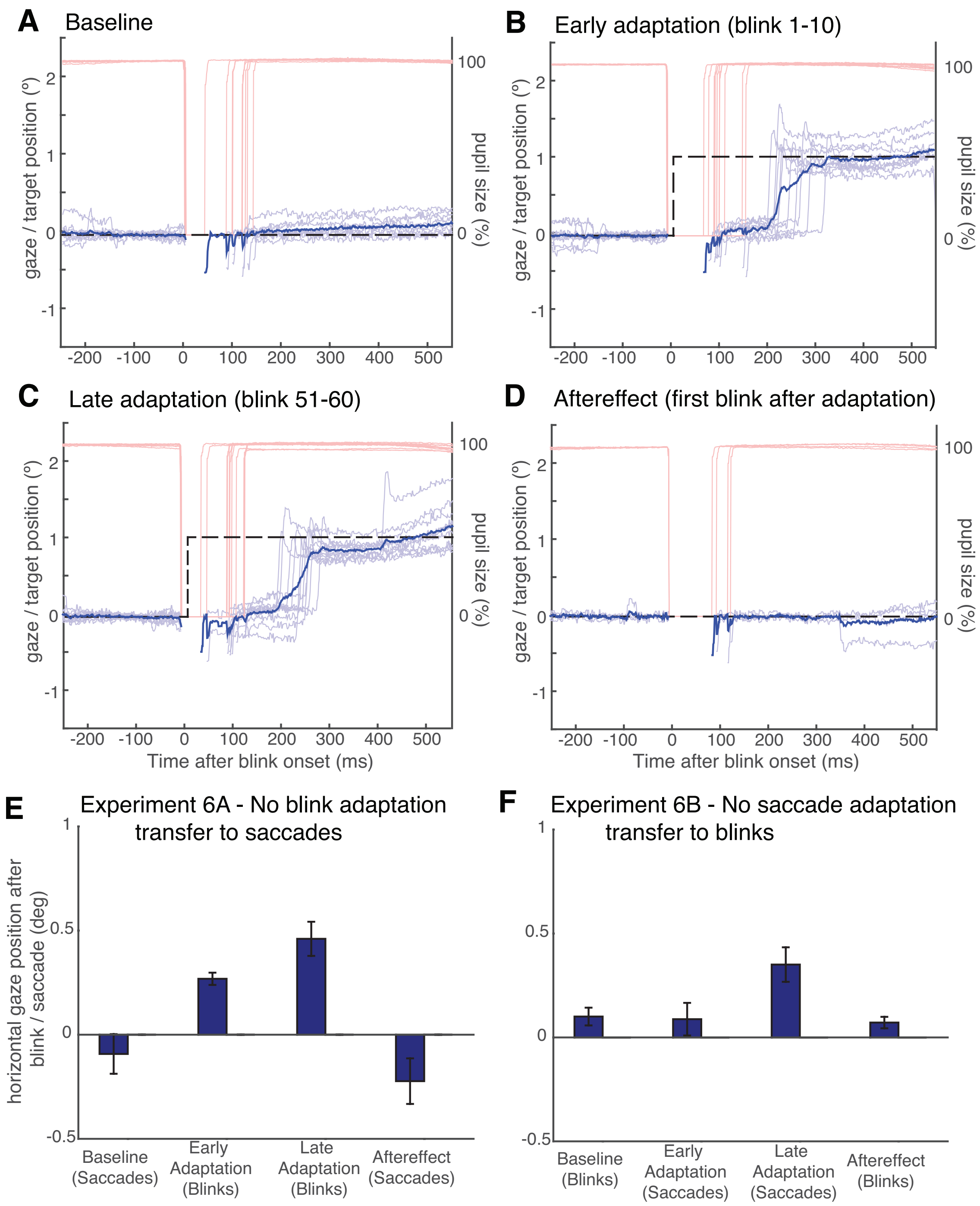

Figure S3. Related to Figures 2 and 3. Results for control experiments.
A – D Gaze position traces from one observer in Experiment 3 (1° target step). The plots show horizontal gaze positions and pupil size around the time of simulated eye blinks (closure of the shutter glasses), plotted in the same way as Figure 2. The shutter glasses cover the pupil far quicker than eye lids do for natural blinks. Noise due to partial occlusion is less prevalent. Dark blue lines show average gaze positions

for 10 blinks (4 blinks in panel D), dashed black lines show target positions. **A** Baseline phase without target steps. Gaze positions after the blink are mostly unperturbed. **B** Early adaptation phase. Gaze direction remains unperturbed after the simulated blink, until saccades re-center the fixation target on the fovea. **C** Late adaptation phase. Gaze position patterns look identical to the early adaptation phase. No adaptation of gaze occurs. **D** No aftereffect occurs either. Gaze patterns with no target steps after adaptation look similar as in the baseline phase.

E – F No transfer of blink adaptation to down-up saccade sequence.

In an additional control we assessed whether blink adaptation also adapts retargeting of saccadic eye movements or vice versa. **E** In Experiment 6A, five observers adapted to 0.5° rightward target steps during a series of 60 blinks, as in Experiment 1. After the adaptation phase, observers performed a quick saccade sequence 1.5° downward and 2° nasally (for the tracked right eye) and back to the original target position (no rightward target step). Gaze positions after each blink in the late adaptation phase (last 10 blinks) were significantly biased towards the anticipated target position ($t(4) = 5.617$, $p = 0.0049$), just as in Experiment 1. After adaptation, the horizontal gaze position after the saccade sequence showed no bias in the direction of the adapted target step during blinks ($t(4) = -2.038$, $p = 0.2447$). **F** In Experiment 6B, five participants performed the same saccade sequence for 60 trials with the final target reappearing in a position stepped 0.5° to the right from its original position. In the late adaptation phase, initial saccade landing positions after the sequence of saccades were significantly biased towards the stepped target ($t(4) = 3.243$, $p = 0.0316$). This saccadic adaptation, however, did not transfer to blinks occurring after the adaptation phase. Initial gaze positions after blinks were not significantly biased ($t(4) = 1.861$, $p = 0.136$).

Supplemental Experimental Procedures

Participants

A total of 13 observers volunteered to take part in the experiments. Three observers were co-authors on the study, ten were completely naïve and did not know that experiments had anything to do with eye blinks. Six observers took part in Experiment 1, three in Experiment 2, six in Experiment 3 (two only participated in the 0.5° condition), five in Experiment 4 (one only participated in the 0.5° condition), and five each in Experiments 5, 6A, and 6B. One participant's data had to be excluded from the analysis in Experiment 1 due to excessive drift in the eye tracker data. All participants had normal or corrected-to-normal visual acuity, and were reimbursed for their participation. The study was approved by institutional review at the Université Paris Descartes and Nanyang Technological University.

Apparatus & Stimuli

Stimuli were projected onto a screen (dimensions: 135 cm by 76 cm) with a PROPixx projector (VPixx Technologies, Saint-Bruno, Quebec, Canada) at 100 Hz image refresh rate. Stimuli were controlled from an Apple Mac Computer running Matlab (Mathworks, Natick, MA, USA) and Psychophysics Toolbox [S1,S2]. Observers were seated 185 cm from the screen with their heads immobilized using a chin and forehead rest. Apart from the stimulus on the screen, the room was completely dark, and the edges of the projection area were not visible. Experiments 5 and 6 were performed using a CRT monitor at 100 Hz refresh rate (Sun Microsystem 21 inch FD premium; visible area 40 cm by 30 cm) with participants seated at a distance of 68 cm. Observers' eye gaze direction and pupil size were monitored using an EyeLink 1000 eye tracker (SR Research, Ottawa, Ontario, Canada) at 1000 Hz. The EyeLink's pupil size estimate was used to detect eye blinks in real-time. Whenever the pupil size dropped by more than 20% in two successive samples (1 ms), we detected the onset of an eye blink. This was used to trigger changes to the stimulus display during the next screen refresh (up to 10 ms later), if the observer's eyelid was closed (i.e., the pupil size was 0).

The stimulus consisted of a single white dot (90 cdm^{-2}) on a dark background (0.05 cdm^{-2}). The dot was a circular disk with a diameter of 0.26° visual angle. When the eye tracker detected the onset of a blink, the dot jumped to a new position, laterally displaced to the right from the last position by either 0.5° visual angle or, in separate sessions of the experiment, 1.0°. To prevent the dot from moving off the screen for repeated blinks, the dot jumped to a random position in the central 10.45° × 7.84° of the screen at random intervals every 3 to 4 s, or when the dot would be more than 7° to the right of the centre of the screen after the next blink. These random jumps did not coincide systematically with observers' eye blinks.

In Experiments 2-4, Plato occlusion spectacles (Translucent Technologies Inc., Toronto, Ontario, Canada) were used to simulate eye blinks by temporally obstructing the observers' view of the screen. The opening and closing of the spectacles was controlled, through an Arduino UNO board, by the same computer controlling stimulus presentation.

Experiment 1 - Blinks

Observers were instructed to simply fixate the dot on the screen and to follow it with their gaze whenever it jumped to different positions. Note that naïve observers were not informed about the systematic target steps triggered by each blink, and they were not instructed to blink in any specific way. In fact, naïve observers were unaware that the experiment had anything to do with eye blinks, and did not report detecting the systematic steps triggered by eye blinks, even after they were debriefed and told of the manipulation. The only target movements they reported were those where the target jumped to new random positions on the screen every 3-4 seconds.

The experiment lasted for a total of 140 blinks. The first 10 blinks were to measure the stability of gaze across eye blinks without target dot displacements (baseline phase). The next 60 blinks were the adaptation phase, in which the target dot was displaced with every blink (adaptation phase). The following 10 blinks again had no target displacements to assess any possible aftereffects of gaze adaptation (aftereffect phase). The remaining 60 blinks consisted of 3 cycles of top-up adaptation with 15 blinks including target steps and 5 blinks with no steps.

Experiment 2 – Simulated blinks with shutter glasses

In Experiment 2 observers were instructed to avoid blinking as much as possible. The occlusion spectacles were used to "replay" a typical blink sequence to the observer by closing the shutters at random intervals for random durations. Intervals and durations were determined from empirical blink data from Experiment 1 (Figure S2). For each observer, we fitted a gamma distribution to the histogram of interval durations between blinks and a Gaussian distribution to the histogram of blink durations as measured for each observer in Experiment 1. These functions were then used to generate a random sequence of intervals and durations to obstruct the view of the screen using the shutter glasses in Experiment 2.

In all other aspects, Experiment 2 was identical to Experiment 1. The same sequence of 140 baseline and adaptation blinks was used. The target displacement occurred while the spectacles occluded the view of the screen.

Experiment 3 – Simulated blinks with warning tone

In Experiment 3, we repeated the same procedure as in Experiment 2, but preceded each closure of the shutter glasses by a warning tone, a 300 Hz pure tone beep that sounded 200 ms before the shutter glasses closed and lasted for 80 ms. All other details were identical to Experiment 2.

Experiment 4 – Voluntarily triggered simulated blinks

To account for the possibility that an efference copy signal that is only elicited by a voluntary action causes the effects of Experiment 1, we repeated Experiment 2 with simulated blinks that were triggered by the observer via a key press. Observers were instructed to press the space bar key on a computer keyboard at random intervals. As soon as the key was pressed, the shutter glasses closed for a random duration drawn from a normal distribution based on empirical blink data, as in Experiments 2 and 3. There was no explicit delay between the key press and the simulated blink, and no warning tone. All other details of the experiment and the sequence of baseline and adaptation phases were identical to Experiment 2.

Experiment 5 – "Mudsplash"-induced change blindness

In Experiment 5, the simulated blink was replaced by the presentation of a random-dot mask stimulus. The target dot disappeared at random intervals (based on empirical blink data from Experiment 1) and was replaced by ~180 dots identical to the target dot, distributed randomly throughout the whole screen area, but sparing a circle of 1.0° radius (in the 0.5° step condition) or 1.5° radius (in the 1.0° step condition) around the position of the fixation target. This mask stimulus was presented for a fixed duration of 200 ms and was then replaced by the new fixation target in its stepped position. All other details of the experiment and the sequence of baseline and adaptation phases were identical to Experiment 2.

Experiment 6 – Transfer of blink adaptation to saccade sequences or saccadic adaptation to blinks

Experiment 6 tested whether blink adaptation could be the result of a sequence of saccades that occurs during a blink and not because of the blink itself. If this were the case, blink adaptation should transfer to saccades that resemble the eye movements made during the blink, or vice versa, adaptation to a target step occurring during a saccade sequence should transfer to subsequent blinks.

Since during blinks, the eyes move disconjugately downwards and nasally, there is no single saccade vector that matches the direction of the blink-related eye movements for both eyes. Therefore, we decided to instruct observers to perform diagonal saccades downwards and nasally for the right eye, which was tracked by the eye tracker, but temporally for the left eye. The original target position was in the central region of the screen, changing positions randomly every 3-4 s, as in the adaptation phase of Experiment 1 (see above). After variable delays (taken from the distribution of inter-blink intervals from Experiment 1) the target dot disappeared, and was replaced by a saccade target 1.5° below and 2° to the left (nasally for the right eye only). These values are based on recent measurements of blink-related eye movements with scleral search coils reported in [S3]. After 200 ms, the saccade target was turned off and the dot reappeared in its original position. Observers performed a diagonal saccade to the target and back up to the original position.

In Experiment 6A, 5 observers first performed 10 saccade sequences as described above for a baseline measurement of saccade accuracy. Then, observers adapted to a 0.5° rightward step consistently occurring during a sequence of 60 consecutive blinks (as in Experiment 1). After the adaptation phase, observers again performed 10 saccade sequences. We analysed the horizontal gaze position after each blink in the adaptation phase and confirmed the occurrence of adaptation, as in Experiment 1. We further analysed the horizontal gaze position after each second saccade back up to the original target position for a potential transfer of adaptation to this retargeting saccade of the down-up sequence. Results are shown in Figure S3E.

In Experiment 6B, we tested whether adaptation to a lateral target step during a saccade sequence resembling blink-related eye movements could transfer to subsequent blinks. Five observers first blinked 10 times (as in the baseline phase of Experiment 1), and then performed 60 saccade sequences as described above. However, the target reappeared not in its original position, but in a position stepped 0.5° to the right to induce an adaptive change to the second saccade of the sequence. After adapting to this step, observers performed another 10 blinks that were analysed for any potential bias in the post-blink gaze position due to adaptation to the step during the saccade sequence. Results are shown in Figure S3F.

Analysis

We plotted eye gaze data time-locked to the onset of a blink (see Figure 2 and S3A-D). We only analysed the horizontal eye gaze position. The average gaze position during the window 150 ms to 50 ms before the detected blink onset was defined as 0°. We were interested in analysing the first gaze position after the blink, as soon as the eyelid opened again. Due to tracker artefacts when the pupil is partially occluded by the eyelid, however, the gaze signal immediately after the blink is perturbed by faulty gaze position signals. We used local eye gaze variance to identify the time point when this noise subsided. The noise was defined to end when the variance of horizontal gaze position within a sliding window of 10 ms duration dropped to below 1.5 times the variance in a window 150 ms to 50 ms before the blink onset. Saccades were detected using a velocity-based algorithm for detection of microsaccades [S4]. All eye position traces were checked manually to correct faulty detection of the end of noise periods and saccades. To determine the first stable eye gaze position after the blink, we then averaged the gaze position between the point when tracker noise subsided until the first detected saccade, or until a maximum duration of 200 ms had passed, whichever was shorter. This average was defined as the post-blink gaze position.

Supplemental References

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