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# Temporal recalibration to delayed visual consequences of saccades

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**The accurate inference of causality between actions and their sensory outcomes requires determining their temporal relationship correctly despite variable delays within and across sensory modalities. Temporal recalibration—the perceptual realignment of actions with delayed sensory feedback—has been demonstrated across various sensorimotor domains. Here, we investigate whether this mechanism extends to saccadic eye movements and sensory events contingent on them. In three experiments, participants made horizontal saccades that triggered high-contrast flashes at varying delays. They then reported whether the flashes occurred during or after the saccade, allowing us to track perceived event timing. Exposure to consistent delays between saccade onset and the flash led to a shift in perceptual reports: flashes presented after saccade offset were more often judged as occurring during the movement. This recalibration effect was robust even when we manipulated relevant visual cues such as the presence of a structured background or the continuity of the saccade target. In a replay condition, we found a significant but much smaller recalibration effect between replayed saccades and flash, demonstrating the importance of action execution for visuomotor temporal recalibration. These findings highlight the visual system's remarkable adaptability to temporal delays between eye movements and their sensory consequences. A similar recalibration mechanism may support perceptual stability in natural vision by dynamically realigning saccades with their resulting visual input, even amid changing visual conditions.**

## Introduction

Sensorimotor contingencies delineate the lawful connection between motor actions and their corresponding sensory consequences (O'Regan & Noë, 2001). This concept is particularly evident for saccades—rapid eye movements that relocate the fovea to the next point of interest. Because each saccade produces a retinal image shift of the same amplitude in the opposite direction and with a velocity profile that scales with saccade amplitude (Bahill, Clark, & Stark, 1975), the kinematics of the resulting retinal motion are highly stereotyped—and indeed our visual system seems precisely tuned to them (Rolfs, Schweitzer, Castet, Watson, & Ohl, 2025). The reliability of this relation appears to be crucial to experiencing continuity in perception in the face of frequent, saccade-induced retinal image shifts. Maintaining this continuity requires the brain to learn the causal relationship between motor actions and their immediate sensory consequences (Kilteni, Houborg, & Ehrsson, 2019;

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Stetson, Cui, Montague, & Eagleman, 2006; Sugano, Keetels, & Vroomen, 2010), which may indeed be fundamental to the development of human causal learning and reasoning at large (Goddu & Gopnik, 2024). However, given the dynamic nature of delays between actions and their sensory outcomes, the temporal aspect of this prediction poses an ongoing challenge. Factors like contrast and luminance influence the speed of visual input processing (Reich, Mechler, & Victor, 2001), introducing variations in processing times (Lennie, 1981; Purpura, Tranchina, Kaplan, & Shapley, 1990). The timing of transients arising from saccade-induced retinal motion will thus vary depending on overall luminance and contrast. Maintaining reliable sensorimotor contingencies, therefore, requires a mechanism ensuring continuous calibration of the temporal relationship between actions and their sensory outcomes.

Temporal recalibration provides one such mechanism. Temporal recalibration refers to the adaptive adjustment of perceived event timing after exposure to a temporal discrepancy between two events, such as between an action and its sensory outcome. It is thought to arise from updates to predictive mechanisms in response to systematic mismatches between expected and actual sensory outcomes and can lead to the perceptual alignment of asynchronous events, or even the reversal of their perceived temporal order (Stetson et al., 2006). In their seminal study, Stetson et al. showed that, after adaptation to a systematic 135-ms delay between button press and flash, participants reported flashes occurring right after button press as having happened before the button was pressed, demonstrating a recalibration of perception to the introduced delay. Similar effects have been observed across various sensory modalities such as audiovisual or audiomotor temporal recalibration (Sugano et al., 2010) and even in self-touch (Fritz & Zimmermann, 2023; Kilteni et al., 2019), indicating that sensory systems flexibly adapt to altered temporal contingencies.

Eye movements present a particularly compelling case for studying sensorimotor timing, given the immediacy of their sensory consequences (Rolfs & Schweitzer, 2022). Yet temporal recalibration during saccades has not been investigated thus far. Eye movements differ from other manual movements in that their immediate sensory consequences are rarely consciously perceived, a phenomenon known as saccadic omission (Campbell & Wurtz, 1978). Not only do the visual consequences of saccades go unnoticed, humans also lack accurate awareness of saccade timing and often predate it (Deubel, Irwin, & Schneider, 1999; Hunt & Cavanagh, 2009). Additionally, as opposed to body movements that make contact with the world, eye movements do not cause any changes in the environment itself, rendering their natural sensory outcomes difficult to experimentally manipulate, especially owing to inherent delays in visual presentation systems (Schweitzer & Rolfs, 2020). To investigate temporal recalibration in the context of eye movements, therefore, we introduced a sensory consequence that is both controllable and perceptually salient: a high-contrast flash occurring at a set delay after saccade onset. In three experiments, participants executed saccades toward a cued location across a patterned background. Saccades triggered a large flash, and participants reported whether they had perceived the flash during the movement or after. To investigate whether temporal recalibration requires the motor act, we also collected perceptual reports in replay sessions. During these sessions, participants fixated the center of the screen and judged the time of flash presentation relative to a background movement that replayed the proximate retinal motion resulting from a saccade. We found that exposure to systematic sensory delays resulted in temporal recalibration: Flashes presented just after saccade offset were now frequently perceived as occurring during the saccade. This finding suggests a perceptual shift comparable with the effect previously observed in other sensory modalities. A similar but smaller shift was seen when replaying the sensory consequences of a saccade to the fixating eye, indicating that this recalibration is partly influenced by visual factors. However, the size of recalibration remained unaltered when the availability of saccade target and background information was varied across trials, suggesting it is driven primarily by other factors, potentially related to internal sensorimotor predictions rather than external visual cues.

# Methods

## Participants

For each experiment, participants were recruited via word-of-mouth and the local subject pool of Humboldt-Universität zu Berlin. All participants had normal or corrected-to-normal visual acuity, tested before the first session using a Snellen chart. The study was conducted in accordance with the Declaration of Helsinki (2013) and approved by the Ethics Committee of the Department of Psychology of Humboldt Universität zu Berlin. Participants gave written consent before inclusion in the study. As compensation, they received either 10€ per hour or study credit points.

## Experiment 1

Nineteen participants were recruited for this experiment. One participant withdrew from the study, and six were excluded owing to low task performance based on the preregistered exclusion criterion (https://osf.io/r7s6k). Specifically, participants were excluded if their psychometric function for the baseline condition in the second session (discussed elsewhere in this article) did not include time points corresponding with response probabilities of 0.25 and 0.75 for the judgment “flash perceived after saccade landing.” Owing to the relatively high exclusion rate, we terminated data collection before reaching the preregistered target of 16 valid datasets. Our aim was to revise the experimental procedure for Experiment 2 to allow for a broader range of subjective reports and thereby reduce participant exclusion. The final sample consisted of 13 participants (9 female; age range, 19–35 years), of whom 8 were right-eye dominant.

## Experiment 2

Thirty-two participants were recruited. Three participants withdrew from the study, and 13 were excluded owing to low task performance. To reduce exclusion and retain more data, we deviated slightly from the preregistered exclusion criterion (https://osf.io/wrx8n) by applying a more lenient threshold: participants were included if their baseline psychometric curves in the second session included time points corresponding with response probabilities of 0.3 and 0.7 for the judgment “flash perceived after saccade landing.” Data collection continued until the preregistered target of 16 valid datasets was reached (11 female; age range, 19–35 years; 9 right-eye dominant).

## Experiment 3

Twenty-seven participants were recruited. Three withdrew from the study, and six were excluded owing to inability to perform the task at a sufficient level. To maximize sample size, we deviated from the preregistered exclusion criterion of requiring the inclusion of response probabilities of 0.3 and 0.7 in the baseline psychometric curve (https://osf.io/gfvp9) and included all complete datasets, resulting in 18 valid datasets. One additional participant was excluded after model fitting (see Methods) owing to poor performance, yielding a final sample of 17 participants (12 female; 11 right-eye dominant; age range, 19–34 years). Although the preregistered target was 16 datasets, we opted to retain all usable data to increase power.

## Apparatus

Experiments were conducted in a dimly-lit room with participants seated 340 cm from the projection screen (250.2 × 141.0 cm, Stewart Silver 5D Deluxe, Stewart Filmscreen, Torrance, CA) with their heads stabilized on a chin rest. A PROPixx DLP projector (Vpixx Technologies, Saint-Bruno, QC, Canada) with a refresh rate of 1,440 Hz and a resolution of 960 × 540 pixels was used to project the stimuli onto the screen. A TRACKPixx3 tabletop system (VPixx Technologies, Saint-Bruno, QC, Canada) was used to track eye movements (binocular) at a sampling rate of 2,000 Hz. The experiment was run on a Dell Precision T7810 Workstation and experimental code was implemented in Matlab 2018b (Mathworks, Natick, MA) using PsychToolbox (Brainard, 1997; Kleiner et al., 2007). Participants responded by pressing the left or right arrow key on a standard keyboard positioned centrally in front of them.

## Stimuli and procedure

### *Experimental procedure*

For Experiments 1 and 2, participants completed three sessions, which differed in trial number and task. In both experiments, the first session was a training (saccade) session to familiarize participants with the task and improve performance during data collection. In saccade sessions (first and second session; Figure 1a), participants performed horizontal saccades across the screen which triggered a flash. In replay sessions (third session; Figure 1b), participants fixated while observing a replay of a previously recorded saccade. Only data collected during the second and third sessions was used for data analysis.

### *Experiment 1*

Before every session, participants completed a training that consisted of 48 trials of the minimum and maximum delay of flash presentation after saccade/background movement onset (approximately 20 ms and 220 ms after saccade onset) in random order. We provided feedback on saccade and perceptual performance after every trial to familiarize participants with the task. Throughout the experiment, timing judgments (see Task procedure for details) were performed on every trial.

*Training (saccade) session*: During the first session, participants completed 30 minutes of the saccade baseline condition (details discussed elsewhere in this article) as an extended training.

*Saccade session*: In the second session, two different probability distributions for flash timings were applied in separate, blocked timing conditions: in 60% of trials flashes appear with an instructed fixed delay of either 0 ms (baseline condition) or 60 ms (delay condition) after saccade onset. Delays for saccade detection and stimulus presentation amounted to approximately

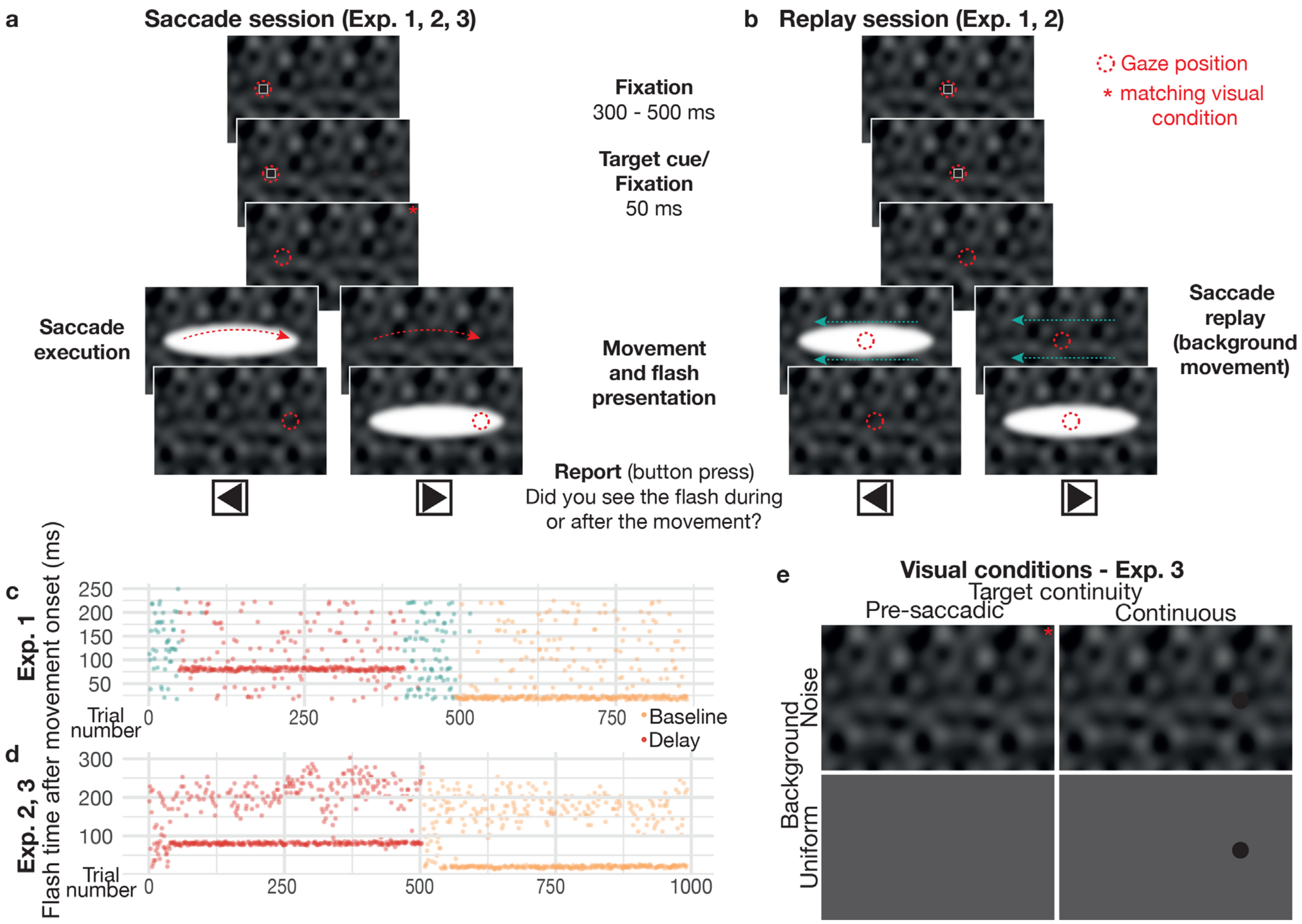

Figure 1. Experimental paradigm. (**a**) Trial structure of the saccade condition. After passing fixation control, a target dot briefly appeared. Participants performed a horizontal saccade which triggered a flash that appeared either during or after the movement. (**b**) Trial structure of the replay condition. Participants fixated the center of the screen throughout the whole trial. The background moved, replaying the retinal consequence of a saccade recorded during the saccade condition. A flash appeared either during or after the movement. (**c**) Flash presentation times in baseline and delay condition for Experiment 1. Participants reported perceived timing after every single trial. Flash times were chosen according to the method of constant stimuli. (**d**) Example for flash times across sessions in Experiments 2 and 3. Participants only reported perceived timing in 40% of the trials. Flash presentation time for these trials was assigned according to a one-up–one-down staircase procedure. (**e**) Visual conditions in Experiment 3 as presented during and after saccade execution. Stimuli in a, b, and e are not drawn to scale.

20.0 ms, leading to an average flash delay of 20.7 ms in the baseline condition and 81.1 ms in the delay condition relative to the onset of the saccade. In the remaining 40% of trials for each condition, flash delays were systematically varied with intended onsets between −40 ms and 160 ms and effective average onsets between −37.1 ms and 158.6 ms relative to saccade offset, respectively.

The session consisted of 2 timing condition blocks of 360 trials. The number of trials was determined by delay times for flash presentation after saccade onset (11 levels), saccade size (2 levels), saccade direction (2 levels), and number of repetitions per delay time depending on the timing condition. Thus, each timing condition contained 240 trials with a fixed delay (2 directions × 2 amplitudes × 60 repetitions) and 120 trials featuring varying flash delay times (2 directions × 2 amplitudes × 10 delay times × 3 repetitions). Before and after the first timing condition block, we presented participants with 33 to 99 trials (132 trials in total) with a uniform distribution of flash times (see Figure 1c). This amounted to a total of 852 trials.

*Replay session*: The final, third session served as a test of the impact of purely visual information on temporal recalibration. Here, observers fixated on a noise background and then judged the timing of the flash against the movement of the background in the two timing conditions (baseline vs. delay). In this session, flash timing, background movement onset and offset were matched with trials from the individual participants' second session to allow for a direct comparison of response distributions in the different delay conditions in saccade and replay session. The background movement in the replay condition matched the saccade in duration and amplitude and features a symmetric velocity profile. For this, the dataset of the saccade session of the same participant was loaded in the beginning of the replay session. After exclusion of invalid trials, the required values were extracted and used in the experiment. Trials where fixation control was unsuccessful were repeated at the end of each block. Thus, the number of trials in the replay session depended on the number of valid trials from the participant's saccade session, as well as the number of repeated trials (average trial number, 865).

### *Experiment 2*

The session structure of Experiment 2 was the same as in Experiment 1. To control for bias toward central tendency and reduce exclusion of participants owing to poor performance respectively, the following two changes were introduced to the experimental procedure. First, dedicated inducer trials (60% of all trials) were used to induce recalibration, and perceptual reports were only collected on the remaining 40% of trials (report trials). Second, flash delays in report trials were adapted to participants' responses by means of a one-up-one-down staircase procedure with a minimum instructed delay of 0 ms and no maximum delay. Step sizes of the staircase were assigned randomly (8.33, 16.66, 25.00, or 33.33 ms) to cover a wide range of timings around perceived movement offset. The saccade experimental session consisted of two timing condition blocks of 460 trials comprising 276 fixed-delay trials (60%) and 184 trials with systematically varied delay (40%). At the beginning of each condition block, to obscure transitions between timing condition blocks, we presented participants with 40 trials with delay times ramping toward the fixed delays (Figure 1d). This amounted to a total of 1,000 trials. The number of trials in the replay condition depended on the number of valid trials collected during the second (saccade) session.

### *Experiment 3*

The experiment comprised four saccade sessions similar to the saccade condition sessions of Experiment 2. The visual conditions (Figure 1e; for details see Trial structure) were presented in a blocked design. Participants completed all four visual condition blocks of 125 trials of one timing condition (baseline or delay) in the first one-half of the experimental session and then continued with the blocks of the other timing condition after a short break. The order of visual conditions was randomized in each timing condition. Each session contained a minimum of 1,000 trials.

## Trial structure

To estimate the perceived time of movement offset, participants made forced-choice temporal order judgments between movement offset and flash.

## Experiments 1 and 2: Movement type: Saccade

On each saccade trial (Figure 1a), the screen was filled with a repetitive noise pattern (luminance, ~12.44 cd/$m^2$; Michelson contrast, 0.5), bandpass filtered to low spatial frequencies between 0.0625 and 0.25 cycles per degree of visual angle to increase motion energy during the movement. A new noise pattern was generated at the beginning of each trial. Patterns repeated with the instructed amplitude of the saccade for the respective trial (14 or 16 degrees of visual angle; dva), ensuring that the image displayed on the screen was identical before and after the movement.

Each saccade trial started with a 0.50-dva square (black with white outline) appearing on one side of the screen and a fixation control (500 ms). The square size was reduced to 0.25 dva upon fixation to provide visual feedback. After passing the fixation control, a second identical square appeared briefly (50 ms) at the opposite side of the screen to indicate the target location. To present stimuli intra-saccadically, we used a previously published detection algorithm and stimulus presentation pipeline (Schweitzer & Rolfs, 2020) that allowed us to present stimuli with a mean minimum latency of 20.7 ms after saccade onset ($k = 2$; $\lambda = 15$; $\theta = 30$).

Saccade detection triggered a 4-ms high-contrast Gaussian ellipse (Weber contrast, ~9.6) displayed either during or after the movement centered on the screen center. The size of the flash (horizontal and vertical standard deviations [SDs] of the Gaussian envelope) was varied randomly across trials to prevent participants from using slight differences in appearance—owing to saccade-induced reductions in contrast sensitivity (Volkmann, Riggs, White, & Moore, 1978) or possibly compression (Ross, Morrone, & Burr, 1997a)—to distinguish intra-saccadic from post-saccadic stimuli presentation times. The vertical SD of the ellipse ranged from 2 to 4 dva and the horizontal SD of the ellipse ranged from 8 to 11 dva. Observers reported whether they perceived the flash before (left arrow) or after movement offset (right arrow) by pressing the respective keys. Saccades were considered correct if they reached the target area (3.5 dva around the target dot), and observers performed not more than one saccade. If eye movements did not pass these criteria, observers received feedback, and the trial was added at the end of the block.

## Experiments 1 and 2: Movement type: Replay

The third session was a replay session with background movement and flash presentation generated trial-by-trial based on the time of saccade latency, onset, offset and flash time relative to saccade offset of the second session (see Session structure) of that participant to assess a putative temporal recalibration effect in a comparable visual-only task. In replay sessions (Figure 1b), participants were instructed to fixate the center of the screen while observing a background movement. The fixation dot was displayed in the center of the screen and, after passing fixation control, the background was moved according to the saccade amplitude (mean ± 95% confidence interval, 13.3 ± 0.3 dva) and saccade duration (60.7 ± 2.2 ms) measured during the matching trial in the saccade session. The background motion featured a Gaussian velocity profile. The Gaussian velocity profile for the simulated saccade was calculated by first defining the duration of the saccade based on the matching saccade trial and calculating sampling time steps based on the frame duration. The position profile was then generated using a normalized cumulative distribution function with a mean of saccade duration/2 (midpoint of the saccade) and an SD of saccade duration/6. The resulting values were scaled by the horizontal amplitude of the saccade to match the desired movement amplitude. In Experiment 1, flashes were presented relative to the background movement based on the respective timing in the matching saccade session of that participant (Figure 1c). In Experiment 2, the flash timing of a subset of trials (the report trials, discussed elsewhere in this article) were assigned based on two staircases, starting at 0 ms and 200 ms instructed flash delay, respectively, with a one-up-one-down-staircase procedure (Figure 1d).

## Experiment 3

The third experiment featured a two-by-two-design of visual conditions (target continuity × background) additional to the two timing conditions to investigate the influence of visual factors in our task (Figure 1e). The trial structure followed the procedure described for saccade trials in Experiments 1 and 2 with small alterations. First, target continuity was manipulated as post-saccadic availability of the target to increase certainty of time of saccade offset. As in Experiments 1 and 2, the target appeared once the participant passed fixation control. In the pre-saccadic target condition, the target disappeared after 50 ms (as in Experiments 1 and 2). In the continuous target condition, the target was displayed until the end of the trial. To add visual information during the eye movement, the target was a black circle with a diameter of 2 dva. Second, we modulated background appearance—it was either uniformly gray (uniform background condition) or patterned (noise background condition) matched for mean luminance as described above for Experiments 1 and 2. Experiments 3 thus had four different visual conditions (uniform background–continuous target, uniform background–pre-saccadic target, noise background–continuous target, and noise background–pre-saccadic target) (see Figure 1e).

## Data analysis

Preprocessing included offline saccade detection using the Engbert–Kliegl algorithm with standard parameters. Eye velocity was calculated from position data (Engbert & Kliegl, 2003). Saccades were detected using a velocity threshold (5 SD), minimum duration (30 samples), and merged if separated by fewer than 10 samples (Engbert & Mergenthaler, 2006). Key saccade parameters were extracted, including saccade onset and offset as well as amplitude. We excluded data from trials in which fixation control was not passed or participants did not reach the target area with a single eye movement. Offline detection for eye movements was implemented in Matlab 2018b (Mathworks, Natick, MA).

All subsequent analyses were conducted using RStudio (RStudio 2024.04.1+748, R version 4.4.0). Data preprocessing, visualization, and hypothesis testing were performed using base R functions and additional packages, including dplyr, version 1.1.4, for data manipulation (Wickham, François, Henry, Müller, & Vaughan, 2014), ggplot2, version 3.5.1, for visualization (Wickham et al., 2007), and lme4, version 1.1.35.3, for mixed-effects modeling (Bates, Maechler, Bolker, & Walker, 2003).

## Experiments 1 and 2

To investigate whether participants report 'during' more often for later stimuli in the delay condition, we calculated and compared point of subjective simultaneity (PSS) values across sessions and conditions. For each participant, we determined the PSS as the time difference between movement offset and flash presentation at which the reported 'flash after movement offset' had a 50% probability. Individual psychometric curves for PSS extraction were fitted with R's 'tidy verse' package (Wickham et al., 2019) using logistic regression to relate participant's responses to the time of the flash in relation to movement offset in that trial.

## Statistical inference

To determine whether the added systematic delay between movement onset and flash presentation led to a significant PSS shift, we performed a repeated-measures analysis of variance (rmANOVA) with timing condition (baseline vs delay) and movement type condition (saccade session vs replay session) as factors for Experiments 1 and 2. Effect sizes were calculated using generalized eta-squared ($\eta^2_G$), which measures the proportion of variance explained by each factor, adjusted for the overall variance in the model (Olejnik & Algina, 2003). When we observed significant interactions, we used pairwise *t*-tests to compare the PSS shift between the different timing conditions for each movement type separately. Additionally, the Bayes factor ($BF_{10}$) was computed to quantify the evidence for the alternative hypothesis (a difference between conditions) relative to the null hypothesis (no difference). We used the ttestBF function from the BayesFactor package in R (Morey & Rouder, 2012), with the Jeffreys–Zellner–Siow prior (Rouder, Speckman, Sun, Morey, & Iverson, 2009). The prior for the effect size was set to a scale parameter of $r = 0.707$, reflecting moderate prior belief in small-to-medium effects.

## Experiment 3

The increased number of visual conditions tested per session led to fewer trials per condition. Due to this, fitting reliable psychometric curves was not possible in some of the conditions. To reduce data loss owing to exclusion, we deviated from the pre-registered analysis plan and used a generalized linear mixed effects model implemented using the 'lme4' package in R with maximum likelihood estimation (Laplace approximation) for Experiment 3. A generalized linear mixed effects model was used to account for the nested structure of the data and the binary nature of the outcome variable.

The model predicted responses based on the fixed effects flash time (continuous), timing condition (baseline vs. delay), target availability (pre-saccadic vs. continuous), and background (uniform vs. noise pattern). Random intercepts and slopes were included for participants and timing condition and to account for variability between individuals and timing conditions. A logit link function was used owing to the binary outcome variable.

# Results

## Experiment 1

### *Systematic delay of sensory consequence leads to temporal recalibration in saccade tasks*

We investigated whether a systematic delay between an eye movement and a contingent stimulus results in perceptual realignment of these two events. By using temporal order judgments between the offset of a saccade and the sensory consequence of the saccade, we determined when participants perceived the stimulus relative to their eye movement. A perceptual realignment of action and sensory consequence would be reflected in a shift of reports in the direction expected from the delay resulting in more frequent 'during' reports for later stimulus presentation times. To quantify temporal recalibration, we extracted observers' points of subjective simultaneity in the two timing conditions (Figure 2a–c).

We found a significant shift in the PSS, mean ± 95% confidence interval: 43.4 ± 18.4 ms, $t(12) = 5.14$, $p < 0.001$, between the baseline and delay conditions, confirming an adaptation to the delay. A Bayesian paired *t*-test yielded a $BF_{10}$ of 132.49, indicating decisive evidence for the alternative hypothesis, confirming reliable temporal recalibration.

Analyses of absolute PSS values, saccade latencies and amplitudes are reported in the Supplementary Material (Supplementary Material S1 – Analysis of absolute PSS values in saccade conditions; and Supplementary Material S2 - Analysis of saccade metrics).

### *Visual replay does not evoke the full extent of temporal recalibration*

In the replay session, participants were presented with replays of their saccades as movements of the background pattern, aiming to isolate the visual component of the task from the motor act. We found a PSS shift of 9.6 ± 11.8 ms in the delay condition which was not significantly different from zero, $t(12) = 1.8$, $p = 0.098$ (Figure 2a–c). A Bayesian paired *t*-test provided inconclusive evidence regarding the difference between conditions ($BF_{10} = 0.97$).

A two-way rmANOVA with timing (baseline vs delay) and movement type (saccade vs replay) as factors revealed a significant main effect of the timing on PSS, $F(1,12) = 27.82$, $p < 0.001$, $\eta^2_G = 0.08$, $BF_{10} = 49.97$, but no main effect of movement type, $F(1,12) = 2.24$, $p = 0.16$, $\eta^2_G = 0.02$, $BF_{10} = 0.71$. PSS values were higher in the delay (90.4 ± 4.4 ms) than in the baseline condition (63.8 ± 4.0 ms). The significant interaction between the two factors, $F(1,12) = 11.44$, $p = 0.005$, $\eta^2_G = 0.04$, highlighted that the PSS shift was larger in the saccade compared with the replay condition (see Figure 2b). Comparing the full model with the additive model using a Bayesian rmANOVA, the data were approximately 4.45 times more likely under the full model, indicating moderate evidence for an interaction between movement type and timing.

We also investigated the effect of movement type and timing on task performance to explore

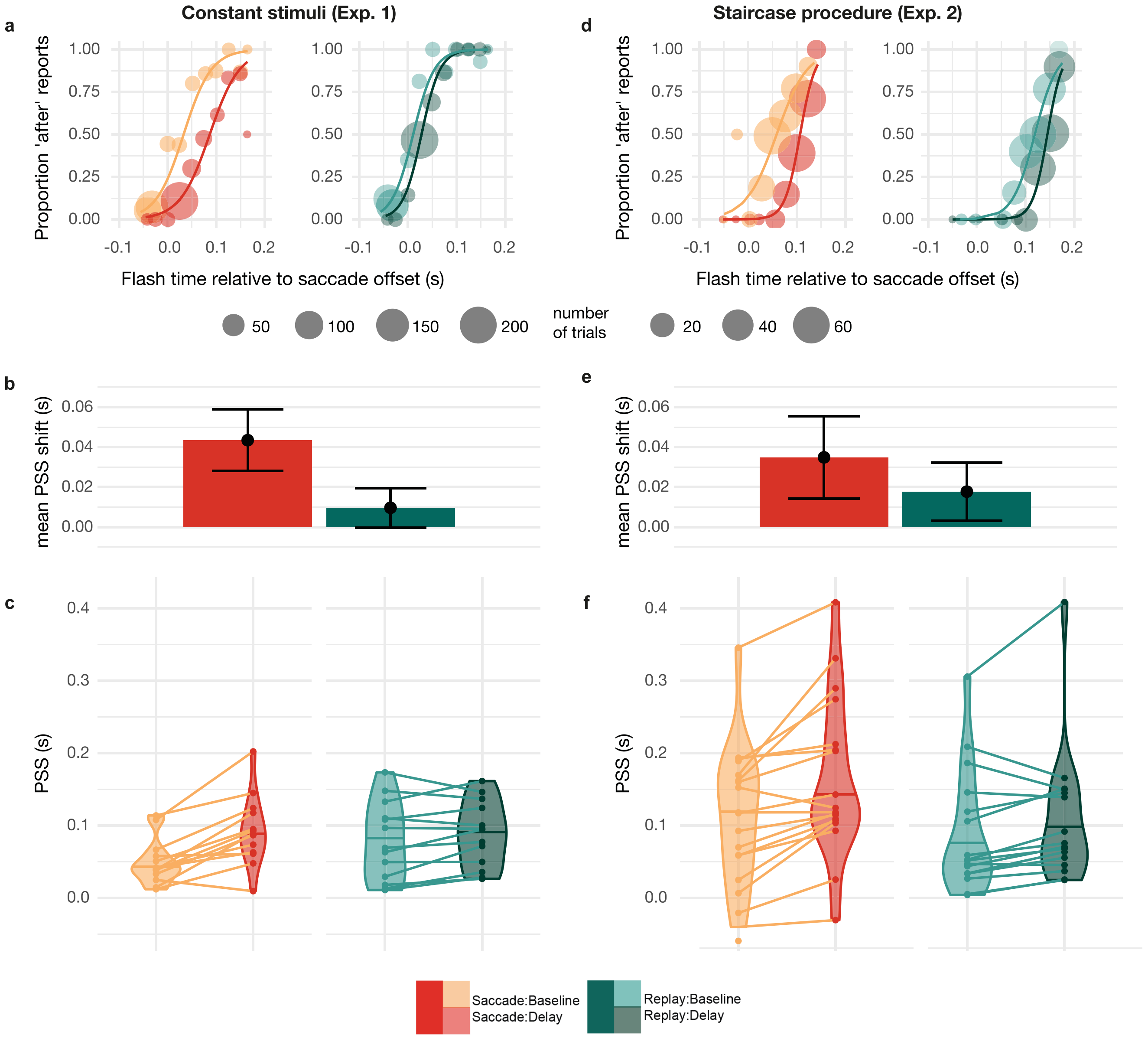

Figure 2. Temporal recalibration in the saccade (red) and replay (green) conditions using the method of constant stimuli (Experiment 1) and a staircase procedure (Experiment 2). (**a**) Data and fitted psychometric functions from an example participant for Experiment 1. Dot size indicates number of trials. (**b**) Mean PSS shift in the saccade and replay conditions in Experiment 1. Error bars indicate 95% CIs. (**c**) Comparison of PSS in baseline and delay conditions in saccade and replay sessions for Experiment 1. Lines connect data points of the same participants. (**d–f**) Results for Experiment 2, analogous to (**a–c**).

performance differences between the conditions. A two-way rmANOVA comparing the slopes of the psychometric functions across sessions and conditions revealed a significant effect of movement type with higher performance in the replay compared with the saccade condition, $F(1,12) = 4.69$, $p = 0.047$, $\eta_G^2 = 0.10$, $BF_{10} = 10.2$, highlighting increased task difficulty in the latter. We found no main effect of timing, $F(1,12) = 0.06$, $p = 0.81$, $\eta_G^2 = 0.00$, $BF_{10} = 0.28$. Although the interaction between timing and movement type was statistically significant, $F(1,12) = 7.04$, $p = 0.02$, $\eta_G^2 = 0.03$, a Bayesian analysis provided no clear evidence for including the interaction term in the model; the models with and without interaction were nearly equally likely ($BF_{10} = 1.02$). This finding could indicate that task performance decreased in the delay condition compared with the baseline condition in the saccade condition, whereas no such decrease was observed in the replay condition.

## Experiment 2

### *Temporal recalibration is not a result of bias toward central tendency*

In Experiment 2, we collected reports only during dedicated report trials (40% of total trials) to rule out the possibility that the temporal recalibration observed in Experiment 1 was influenced by participants strategically balancing their responses across trials. Because most flashes were presented with the inducer delay, such central tendency could have produced a similar shift in responses toward the time point of the inducer delay. In Experiment 2, flash presentation times for report trials were assigned based on a one-up-one-down staircase procedure with varying step sizes. This strategy ensured balanced responses and maximized the number of trials along the slope of the psychometric function. Additionally, this approach allowed the inclusion of participants whose PSSs would have fallen outside a predefined flash presentation time window.

The main findings from Experiment 1 were replicated in Experiment 2 (Figure 2d–f). We found a significant effect of timing (baseline vs delay) on PSS, $F(1,15) = 15.04$, $p = 0.001$, $\eta^2_G = 0.04$, $BF_{10} = 5.25$. Although we found a statistically significant interaction between movement type (saccade vs replay) and timing, $F\,(1,15) = 6.73$, $p = 0.02$, $\eta^2_G = 0.01$, the Bayesian comparison between models with and without the interaction provided only anecdotal evidence against including it ($BF_{10} = 0.64$), likely owing to the small effect size. There was no main effect of movement type, $F(1,15) = 1.70$, $p = 0.21$, $BF_{10} = 0.95$. Put differently, we found a significant PSS shift for both movement types, but the PSS shift was greater in the saccade, 39.4 ± 26.6 ms, $t(15) = 3.96$, $p = 0.001$, $BF_{10} = 31.38$, compared with the replay condition, 18.0 ± 17.7 ms, $t(15) = 2.17$, $p = 0.047$, $BF_{10} = 1.58$. The PSS shift in the replay condition was attenuated after a potential outlier (who had a much larger PSS values than other participants) was excluded, 12.3 ± 13.8 ms, $t\,(14) = 1.90$, $p = 0.078$, $BF_{10} = 1.09$, although the direction of the effect remained the same. The PSS shift in the saccade condition remained largely unaffected by the exclusion, 41.9 ± 22.9 ms, $t\,(14) = 3.96$, $p = 0.001$, $BF_{10} = 26.9$. Across both analyses, the Bayesian evidence remained anecdotal, suggesting that the data do not strongly favor either hypothesis.

Comparing task performance as measured by the slope of psychometric functions, we found a significant effect of movement type with higher task performance in the replay compared with the saccade condition, $F(1,15) = 20.62$, $p > 0.001$, $\eta^2_G = 0.13$, $BF_{10} = 1674.15$, but no main effect of timing, $F\,(1,15) = 2.08$, $p = 0.17$, $BF_{10} = 0.55$, and no interaction between the two factors, $F(1,15) = 1.14$, $p = 0.30$, $BF_{10} = 0.39$.

Finally, we found greater variance in PSSs in Experiment 2 (PSS range, −40.4 to 408.9 ms) than Experiment 1 (PSS range, 9.1 to 202.3 mms) (cf. Figure 2f), owing to the wider range of possible flash presentation times.

Analyses of saccade amplitudes and latencies are reported in the Supplementary Material (Supplementary Material S2 - Analysis of saccade metrics).

## Experiment 3

### *Visuomotor temporal recalibration of saccades occurs independently of target availability and background pattern*

Previous research has indicated that participants often fail to accurately report the timing of their eye movements, indicating a high level of uncertainty regarding the onset and offset of these movements. Consequently, individuals may rely on visual rather than motor cues to perform the assigned temporal order task. In the experimental paradigm presented here, an increase in visual certainty might increase certainty about the time of movement offset, potentially reducing temporal recalibration. This result would be consistent with the hypothesis that the motor event, rather than the sensory event, is the element that is perceptually shifted in time during adaptation (Sugano et al., 2010). To investigate the impact of visual certainty on temporal recalibration, Experiment 3 used a two-by-two design (Figure 1e), manipulating the visual information available during the task by varying the background (uniform vs noise background) and the target continuity (pre-saccadic vs continuous).

We fitted a generalized linear mixed effects model to the data and PSS values were derived from the obtained fits (Figure 3a, see Methods). A three-way rmANOVA with timing, target continuity, and background revealed significant main effects of target continuity, $F(1,16) = 22.19$, $p < 0.001$, $\eta^2_G = 0.06$. and timing, $F\,(1,16) = 28.14$, $p < 0.001$, $\eta^2_G = 0.07$, on PSS values (Figure 3b). We found systematically higher PSSs for conditions with a continuously present target indicating that increased visual certainty about the target was associated with a greater perceived time difference between both events. Alternatively, the presence of the target might have directed participant's attention toward visual cues rather than their motor feedback which may have influenced their reports.

Significant PSS shifts between baseline and delay conditions were observed in all four visual conditions (Figure 3c) with BFs strongly supporting the presence of a significant temporal recalibration effect confirming the results from Experiment 1 and 2. These shifts were slightly smaller in conditions with

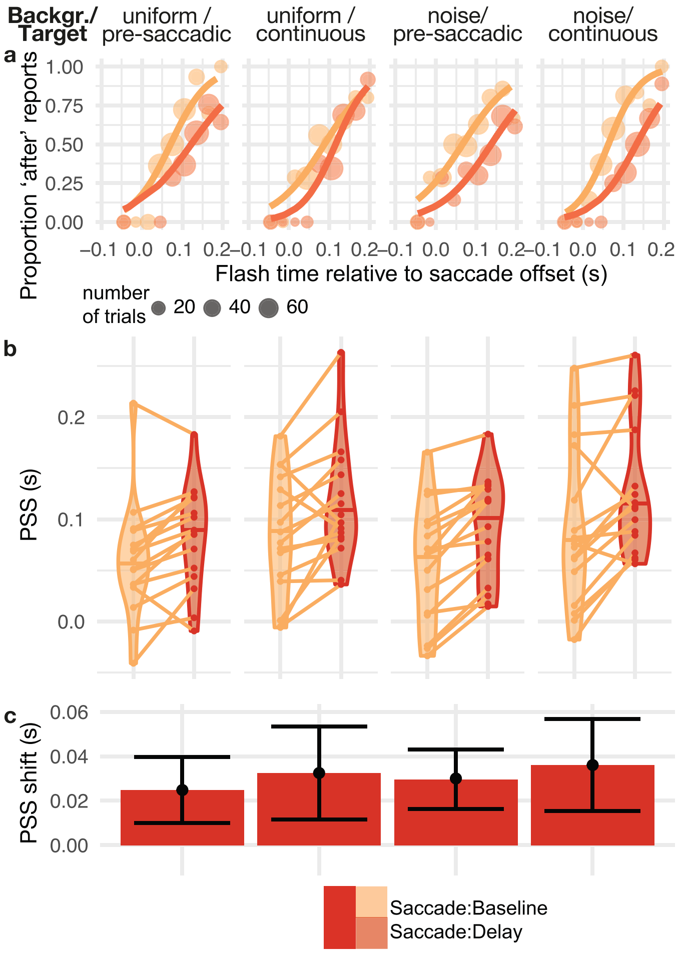

Figure 3. Influence of visual factors on perceived saccade offset and temporal recalibration. (**a**) Data from an example participant for Experiment 3 for four visual conditions (background/target: uniform/presaccadic, uniform/continuous, noise/presaccadic, and noise/continuous). Psychometric function and binned data where dot size indicates the number of trials. (**b**) Mean PSS shift for the different visual conditions in Experiment 3. Error bars indicate 95% CIs. (**c**) Comparison of PSS in the baseline and delay conditions for the four visual conditions. Lines connect data points of the same participants.

a presaccadic presented target, uniform background: 26.9 ± 15.4ms, $t(16) = 3.69$, $p = 0.002$, $BF_{10} = 21.14$; noise background: 30.3 ± 13.9 ms, $t(16) = 4.60$, $p < 0.001$, $BF_{10} = 109.6$, compared with conditions with a continuously presented target, uniform background: 33.0 ± 21.2 ms, $t(16) = 3.30$, $p = 0.005$, $BF_{10} = 10.4$; noise background: 37.4 ± 21.5 ms, $t(16) = 3.68$, $p = 0.002$, $BF_{10} = 20.7$; however, this difference was not significant. All other effects and interactions were insignificant ($Fs < 0.80$; $ps > 0.3$).

With respect to task performance, that is, measured by the slopes of psychometric functions, there was no indication of no significant differences between conditions, $Fs < 2.7$, $ps > 0.12$) suggesting that visual conditions did not systematically reduce the difficulty of the temporal order judgments. A Bayesian repeated-measures ANOVA provided moderate evidence for an effect of condition ($BF_{10} = 1.79$), while models including additional factors or interactions were less supported compared with the null model.

To determine whether target availability and background pattern influence eye movement accuracy, we first examined the density of saccade landing positions (Figure 4a) and found a higher concentration of landings near the target when it remained visible. We quantified this observation by comparing the amplitude of eye movements across conditions (Figure 4b). A three-way rmANOVA with factors timing, target continuity, and background revealed a significant main effect of target continuity, $F(1,16) = 30.25$, $p < 0.001$, $\eta^2_G = 0.11$, $BF_{10} > 10^6$, on saccade amplitudes. Saccade amplitudes were greater in conditions with a continuous target landing closer to the target position demonstrating that participants can use the additional visual information to improve saccade performance—likely owing to reduced spatial uncertainty and cognitive load compared with memory-guided saccades. None of the other effects and interactions were significant, $Fs(1,16) < 0.68$, $ps > 0.419$, $BF_{10} < 0.19$. Analyses of saccade latencies are reported in the Supplementary Material (Supplementary Material S2 - Analysis of saccade metrics).

Taken together, these findings demonstrate that participants use visual cues, particularly a continuously presented target, to guide saccade execution and may also use it to determine the time of their eye movement, as evidenced by larger absolute PSS estimates found for continuously present targets. Yet, temporal recalibration does not depend on the availability of post-saccadic visual information—or the absence thereof.

## Discussion

Across three experiments, we found evidence for temporal recalibration for saccade-contingent sensory consequences. After exposure to systematic sensory delays, flashes presented right after saccade offset were more often reported as occurring during the saccade than before exposure to the delay. This finding is consistent with a perceptual shift of the sensory consequence (the flash) toward the action that caused it (the saccade onset) previously found in other sensory modalities (Stetson et al., 2006; Sugano et al., 2010). A smaller effect was also observed when replaying the sensory consequences of a saccade, suggesting a possible contribution of visual factors, although evidence was limited. Manipulating the availability of visual information during the task did not diminish the effect, demonstrating that recalibration is robust to

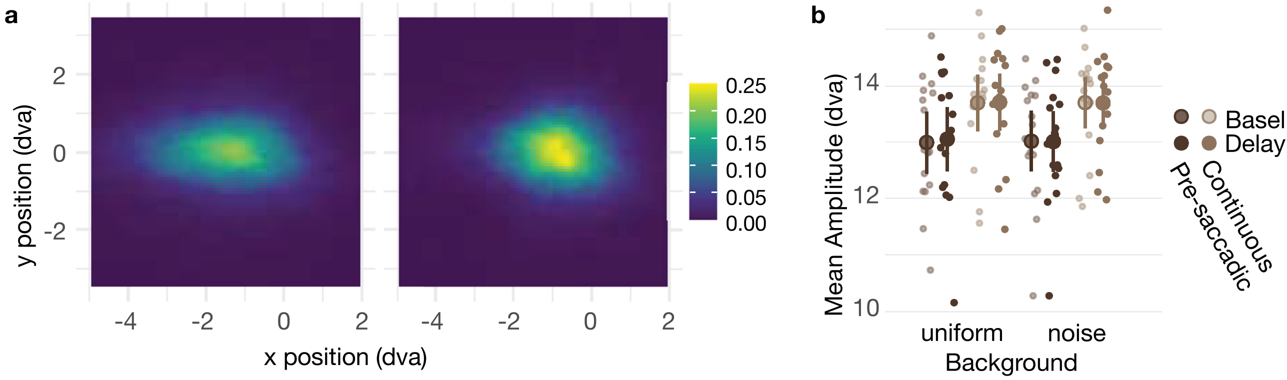

Figure 4. Visualization of saccade metrics. (**a**) Heatmap displaying the two-dimensional kernel density estimation of landing positions relative to target positions to illustrate saccade accuracy for trials with pre-saccadic (left) and continuous (right) target presentation. The colour contours represent density levels, with warmer colors indicating regions of higher data concentration. (**b**) Saccade amplitudes across conditions.

variations in the availability of target and background information.

These results provide evidence that, despite the limited awareness of and voluntary control over eye movements (Klanke, Ohl, & Rolfs, 2025), systematic sensory delays associated with these motor acts are rapidly learned and lead to a recalibration of the perceived timing of their sensory consequences. In our experiments, the size of this effect (~37 ms average across all experiments) was approximately one-half the size of the induced systematic delay (60 ms), which is larger than those found in comparable studies of manual actions, which reported relative effect sizes of 30% to 40% (Stetson et al., 2006; Sugano et al., 2010). This finding raises the possibility that reduced awareness of the eye movement itself may contribute to stronger temporal recalibration. However, the absolute magnitude of the temporal recalibration effect is similar across studies (here, 25–45 ms), potentially reflecting a hardwired limit that is consistent across sensory modalities.

Previous studies using manual responses have generally found little or no temporal recalibration in passive conditions as compared with active ones (Kilteni et al., 2019; Stetson et al., 2006). However, a recent functional magnetic resonance imaging study (Kufer, Schmitter, Kircher, & Straube, 2024), exposed participants to delayed or undelayed visual stimuli triggered by active or passive button presses (i.e., the button was pulled down passively by compressed air while the participant's finger rested on it). Recalibration was tested using delay detection tasks with both visual and auditory outcomes. The study found that temporal recalibration occurred across both modalities, but an active advantage emerged only for visual stimuli. Cerebellar activity supported general recalibration, whereas the frontal and cingulate regions contributed specifically to action-related and cross-modal (vision-to-audition) adjustments, suggesting distinct neural contributions of sensorimotor and inter-sensory processes. In our passive condition, we used replays based on saccadic eye movements and found a modest but consistent shift in perceived simultaneity. Although sensitive to individual variability, its direction aligns with the notion that purely perceptual disruptions can trigger temporal recalibration. The saccade replay involved a whole-screen background shift designed to closely simulate the timing of the motion produced by saccades, which may have engaged the perceptual system in a manner similar to the saccade condition. Previous studies have shown that simulated saccades can evoke some perceptual effects of saccades, such as perisaccadic mislocalization (Ostendorf, Fischer, Gaymard, & Ploner, 2006) or the perceptual omission of retinal motion and motion streaks (Rolfs et al., 2025; Schweitzer et al., 2025). Likewise, Zimmermann, Born, Fink, and Cavanagh (2014) showed that spatial and temporal compression can arise from masking events that interrupt visual input, independent of motor execution. They attributed these effects to a general correspondence process linking targets across transient disruptions. Our saccade replay may have engaged a similar mechanism indicating that motor signals are not strictly necessary for recalibration, though they may sharpen temporal predictions and enhance the effect.

It is important to acknowledge the limitations of the saccade replay. Although we matched the timing of both sessions as closely as possible, the visual stimulation differed in important aspects. During an actual saccade, screen borders move across the retina, generating a motion signal that might have contributed to the temporal recalibration. Additionally, our stimuli replayed only the horizontal component of the saccade, neglecting any oblique components. It is also plausible that temporal recalibration might be more pronounced if the replay condition more closely mimicked the dynamics of retinal motion during an actual saccade. Future studies could explore this by incorporating a shifting frame in the replay condition or by avoiding screen borders altogether to better replicate the visual motion experienced during a saccade.

Interestingly, unimodal temporal recalibration in the visual domain has been reported before, suggesting that the observed effect could also be a visual-only effect, unrelated to the underlying action that was replayed. Arnold and Yarrow (2011) demonstrated temporal recalibration using simultaneity reports in the context of background movement and color changes. In their study, participants judged whether a direction change in background movement coincided with a color change in the background. The authors attributed this effect to mechanisms related to the processing of dynamic visual stimuli. A similar mechanism might be at play in the replay condition of our study, where the background movement could have served as a temporal cue, leading to the observed recalibration.

Task performance was better in the visual-only replay condition compared with the visuomotor saccade condition, indicating greater levels of uncertainty associated with temporal estimates for eye movements compared with visual stimuli. These differences are in line with the transient suppression of visual sensitivity around saccades (Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009; Ross, Morrone, Goldberg, & Burr, 2001; Volkmann et al., 1978), which would lead to shallower psychometric slopes during the saccade condition. Moreover, attention is typically bound to the saccade target just before and during eye movements (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Rolfs & Carrasco, 2012), whereas in the replay condition, attentional resources can be fully allocated to the timing judgment. Together, these factors likely contribute to the reduced precision observed in the saccade condition.

A persistent limitation across experiments was the high rate of participant exclusion owing to insufficient variability in perceptual judgments in the saccade condition. In Experiment 1, a relatively narrow time window for flash presentation around saccades led to the exclusion of participants whose PSS fell outside the tested window, indicating that fixed stimulus sets may not accommodate inter-individual differences in temporal perception. In Experiment 2, we introduced a staircase procedure to address this. However, this concentrated trials near the psychometric slope, likely increasing perceptual uncertainty and task difficulty. Additionally, in Experiment 3, the combination of multiple visual conditions presented across four sessions may have introduced session-dependent variability and noise. Taken together, these findings suggest that the task—requiring precise temporal judgments about trans-saccadic visual events—is cognitively demanding and sensitive to individual differences in perceptual precision and sensorimotor timing. However, because temporal recalibration in natural contexts would occur in the absence of explicit perceptual judgments, the underlying mechanism may still function effectively in natural, unconstrained settings despite difficulties of capturing it experimentally. Future work may benefit from more adaptive and individualized procedures or extended training to improve data retention.

We hypothesized that, owing to this greater uncertainty in the motor domain, participants might rely primarily on visual information to inform their temporal order judgments, even in the visuomotor task. The availability of visual information, such as a continuously present target meant to reduce uncertainty about movement offset, could therefore modulate both their perceived time of movement and temporal recalibration. If additional visual information increases the certainty of movement offset, it might also reduce temporal recalibration if participants could be less likely to shift their perceptual timing. Indeed, it has been previously shown that motor adaptation can be modulated based on the certainty of available visual feedback; for instance, motor adaptation rates in a reaching tasks were higher when visual feedback was less noisy (Wei, 2010) with greater consistency leading to faster adaptation (Gonzalez Castro, Hadjiosif, Hemphill, & Smith, 2014), and saccadic adaptation is stronger when error variability is reduced (Cassanello, Ohl, & Rolfs, 2016; Cassanello, Ostendorf, & Rolfs, 2019; Havermann & Lappe, 2010). However, Souto, Gegenfurtner, and Schütz (2016) found saccade amplitude adaptation to be independent of visual uncertainty in a two-step paradigm where variations in target contrast did not influence adaptation rates (Souto et al., 2016). In our study, target availability significantly affected PSS values—indicating that visual information is used to determine the time of eye movement offset—although temporal recalibration was not affected, suggesting that it may operate independent of the reliability of visual feedback.

It has been noted that effects in timing perception studies may have their origin in shifts of criteria or neural timing (Yarrow, Jahn, Durant, & Arnold, 2011), meaning they could be related solely to decision-making rather than perception. Memory-related contributions, similar to those experienced for temporally proximal events in real-life episodes (Jeunehomme, Leroy, & D'Argembeau, 2020; Uitvlugt & Healey, 2019), could also play a role. An electroencephalographic study investigating the neural correlates of sensorimotor temporal recalibration using a temporal order judgments between a finger tap and a flash found that the effect involves modulation of early perceptual levels of visual processing as well as a high-level, supra-modal recalibration mechanism (Stekelenburg, Sugano, & Vroomen, 2011). In the context of saccades, one candidate signal for anchoring the perceived timing of movement is the efference copy, though proprioceptive and visual cues may also play a role. If recalibration shifts the internal timing of this signal, it could potentially affect the timing of perisaccadic phenomena, such as mislocalization (e.g., Honda, 1989; Ross, Morrone, & Burr, 1997b) or the reduction in contrast sensitivity (Diamond, Ross, & Morrone, 2000), leading them to occur earlier or later than usual. Investigating the time course of these perceptual effects following recalibration could help determine the level at which the shift occurs. Combining such approaches with electroencephalography in the current visuomotor paradigm may offer a promising route to further dissociate perceptual from decisional contributions.

The subjective time of saccade offset observed in our experiments differs from the previous studies, which concluded that the perceived gaze position shifts before the eye movement (Deubel et al., 1999; Hunt & Cavanagh, 2009). However, in our no-delay baseline conditions, PSS values were significantly biased to after saccade offset (see Supplementary Material S1). These discrepancies likely reflect differences in experimental design. The design used here featured flashes presented on the saccade path only after saccade onset, whereas previous studies frequently used stimuli presented at the saccade target location before or after saccade execution. Additionally, participants in our experiments were prompted to judge the time of the flashes as either ‘during’ or ‘after’ the movement, which likely biased their judgments toward later timepoints. Absolute timing values should, therefore, not be overinterpreted. However, because this bias should apply to all conditions alike, it does not affect comparisons between delay conditions.

Our study complements findings in spatial and chromatic aspects of saccade-related perceptual modulation. One study demonstrated that detection thresholds for intra-saccadic displacements can be modulated by the context of previous trials, such that prior exposure to specific visual conditions (e.g., intra-saccadic vs. post-saccadic disturbances) influences the ability to detect subsequent intra-saccadic displacements (Zimmermann, 2020). Another study demonstrated that saccadic suppression can be attenuated during learning, with gradual reductions in its magnitude over time, effectively silencing it when behaviorally advantageous without altering saccade characteristics (Scholes, McGraw, & Roach, 2021). This context-dependent modulation of saccadic suppression highlights the dynamic nature of sensorimotor integration during saccades, where the visual system adapts to minimize the perceptual impact of saccadic disturbances based on prior experiences and task demands (Zimmermann, 2020). Relatedly, Bompas and O’Regan (2006) provided evidence that even color perception can become contingent on eye movements: after prolonged exposure to spectacles that artificially linked gaze direction with chromatic shifts (left visual field appearing blue, right yellow), observers reported systematic color biases (e.g., white appearing bluish during rightward and yellowish during leftward saccades) once the spectacles were removed. These direction-contingent effects on perceived color depended on the amount of eye movement during exposure and could not be explained by simple retinal adaptation or side-based associations, supporting the idea that perceptual systems remain continuously tuned to sensorimotor contingencies (O’Regan & Noë, 2001). To our knowledge, ours is the first study to explore the modulation of the temporal relationship between saccades and resulting sensory input, contributing to a more comprehensive understanding of how sensory and motor information is integrated during rapid eye movements.

Overall, these findings provide evidence that the visual system is remarkably adaptable to temporal changes in visual input contingent on eye movements. Visuo-motor temporal recalibration of saccades was robust to variations in visual cues, suggesting that this mechanism can reliably perceptually realign saccades and their immediate visual consequences—rapid retinal image shifts. Temporal recalibration, therefore, could help to facilitate visual processing despite changing delays in the visual system.

*Keywords: adaptation, saccades, temporal recalibration*

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