american physiological society

JNP JOURNAL OF NEUROPHYSIOLOGY

J Neurophysiol 127: 1655–1668, 2022.
First published June 1, 2022; doi:10.1152/jn.00076.2022

RESEARCH ARTICLE

Control of Movement

Timing and kinematics of horizontal within-blink saccades measured by EOG

Johannes Kirchner,[1,2] Tamara Watson,[3] Niko A. Busch,[1,2] and Markus Lappe[1,2]

[1]*Institute for Psychology, University of Münster, Münster, Germany;* [2]*Otto-Creutzfeldt Center for Cognitive and Behavioural Neuroscience, University of Münster, Münster, Germany; and* [3]*School of Psychology, Western Sydney University, Penrith, New South Wales, Australia*

Abstract

Eyeblinks are the brief closures of the lid. They are accompanied by a cocontraction of the eye muscles that temporarily pulls the whole eyeball back into its socket. When blinks occur together with execution of saccadic gaze shifts, they interfere with the saccadic premotor circuit, causing these within-blink saccades to be slower than normal and also time-locked to blinks. To analyze the trajectory of within-blink saccades, subtraction of the entangled blink-related eye movement is required. Here we propose a combination of principal component analysis (PCA) and a regression model to subtract the blink-related component of the eye movement based on the respective blink metrics. We used electrooculography (EOG) to measure eye and lid movements of 12 participants who performed saccades with and without blinks. We found that within-blink saccades are slower than without-blink saccades and are tightly coupled in time to blink onset. Surprisingly, in some participants we observed large dynamic overshoots of up to 15° for saccades of only 5° amplitude. The finding of dynamic overshoots was independently confirmed by dynamic MRI for two of the participants and challenges the current view that within-blink saccades are programmed as slow, but straight, saccades. We hypothesize that the dynamic overshoots could be attributed to inhibition of omnipause neurons during blinks, the simultaneous cocontraction of extraocular muscles, or a combination of both.

NEW & NOTEWORTHY This study observed that people make large dynamic overshoots when making a saccadic eye movement within a blink but their eyes are back on target by the time the eyelids are open. We used electrooculography (EOG) to measure eye movements even when the lid is down and introduced a novel procedure to subtract blink-related EOG components. These findings challenge the current view that within-blink saccades are programmed as slow but straight saccades.

blink; EOG; eye movement; saccade

INTRODUCTION

Blinks occur in response to threats to the eye and help in maintaining a clear and healthy cornea by spreading a tear film and removing irritants from its surface (1). Blinks are accompanied by a blink-specific movement of the eye called a blink-related eye movement (BREM). Although blinks regularly occur in tandem with saccades, particularly when making large gaze shifts, the BREM is very different from those undertaken when the eyes are open. Many species like rabbits, cats, and guinea pigs have a specific muscle, the retractor bulbi, that pulls the eyeball back into its socket during a blink (2, 3). Humans do not have such a muscle, but it has been shown that their eyeball also retracts and lifts by up to 2 mm during a blink, presumably caused by cocontraction of several extraocular muscles (2, 4). Besides this translational motion, short blinks in humans are also accompanied by a loopy rotational motion typically in the range of 1–5° (4–6).

Although we make many blinks per minute, lasting ~300 ms each, we are unaware of the inevitable loss of vision that is caused by blinks. Active visual suppression occurs during blinks such that the loss of vision goes mostly unnoticed (7). Saccades, which result in disruptive high-velocity motion across the retina, also evade our awareness and are associated with suppression of the visual system. Saccades are often accompanied by blinks, presumably to reduce the overall downtime of vision caused by their disruption by as much as possible (8, 9). Suggestively, the oculomotor system has been shown to use the downtime of vision during blinks

Correspondence: J. Kirchner (johannes.kirchner@uni-muenster.de).
Submitted 25 February 2022 / Revised 31 May 2022 / Accepted 31 May 2022

to correct fixation errors (10), anticipate target movements (11), and reset torsional displacements (12).

The trajectories of eye movements, in particular saccades, have been shown to be altered if they occur together with blinks, which cannot be explained by the superimposed BREM (13, 14). Within-blink saccades have lower peak velocity than those without a blink, and the time of saccade onset is tightly coupled to blink onset. The altered kinematics have been hypothesized to be caused entirely by blink-induced changes to the saccade premotor circuit and not by mechanical interference at a muscular level due to simultaneous cocontraction. Indeed, blinks have been shown to interfere with the generation of saccades in at least two separate locations in the brain stem premotor circuit. First, omnipause neurons (OPNs) in the pons are inhibited shortly after onset of the BREM (15). Second, blinks are associated with a reduction of burst neuron activity in the superior colliculus (SC) (16). OPNs gate the saccadic system by discharging at a tonic rate, so it has been proposed that their inhibition during blinks initiates a premature saccade with reduced velocity (9, 14). This would explain the tight temporal coupling between blinks and saccades, which has been observed in several experiments with reflex blinks (9, 13, 17). It remains unclear whether the same holds true for voluntary blinks (18). Decreased activity in SC burst neurons on the other hand would explain the reduced peak velocity of within-blink saccades. Modeling of the premotor circuit showed that the eye movement that occurs during joint blink and saccades could be understood as a superposition of the loopy BREM and a slow but straight saccade (19). Therefore, the two most prominent features of within-blink saccades, the reduced peak velocity and the time-locking to blink onset, can be explained by changes to the premotor circuit. However, it cannot be ruled out that the cocontraction of extraocular muscles during blinks influences the saccade trajectory on top of the aforementioned changes to the premotor circuit. To analyze timing and kinematics of within-blink saccades, it is important to extract the saccadic gaze shift from the blink-related components. There is currently no systematic approach to achieve this, so here we propose a combination of principal component analysis (PCA)and regression model to account for the BREM trajectories of blinks with variable durations and amplitudes.

The majority of research into within-blink saccades for both monkeys and humans has been conducted with scleral search coils (13, 17, 18, 20, 21). Although search coils have very high spatial and temporal accuracy for measuring eye movements, they typically require ophthalmic anesthesia to be worn comfortably by human participants. Electrooculography (EOG) is a noninvasive method capable of simultaneously measuring eye and lid movements at high temporal resolution (8). EOG used to be a popular tool for measuring eye movements a few decades ago but has been mostly abandoned in favor of video-based methods. Compared with video-based methods, EOG is less precise because it also picks up unwanted data sources and is subject to a baseline drift (22). However, unlike video-based methods it allows noninvasive recordings while the eyes are closed, which is essential for blink research and research, for example, of rapid eye movements during sleep.

In the present study, we collected blink and saccade data from 12 participants over two sessions with binocular EOG. Simultaneous video-based eye-tracker recordings allowed us to estimate and subtract the EOG baseline drift in order to get rid of the main source of corruption in the EOG data. Vertical EOG channel data were used for precise determination of blink metrics such as onset, offset, and amplitude. Crucially, we devised a mathematical procedure to subtract the blink-related signal from horizontal EOG channel data, such that we ended up with only the EOG data associated with the horizontal within-blink saccade. This allowed us to analyze the kinematics and timing of within-blink saccades and directly compare them to saccades without blinks.

METHODS

Participants

Twelve healthy participants (*P1–P12*; age 20–29 yr, 7 males, 5 females) took part in this study and were tested in two sessions on separate days. All participants gave written informed consent and had normal or corrected-to-normal vision. Procedures were approved by the ethics committee of the Department of Psychology and Sports Science of the University of Münster.

Experimental Setup

The experiment took place in a dimly lit room that is specifically designed for EEG experiments. Participants sat at a distance of 86 cm from a 24-in. Viewpixx LCD screen (120 Hz refresh rate, 1,920 × 1,080 pixel resolution), with their head placed on a chin rest to reduce head movements. Stimuli were black dots (0.3° diameter) on a gray background, which were generated with MATLAB R2019a (The MathWorks, Natick, MA) and the Psychophysics Toolbox (23). Auditory cues were beeps of 500-Hz frequency and 100-ms duration.

Video-based eye-tracking.

Gaze position and pupil area of both eyes were recorded with an EyeLink 1000 (SR Research, Mississauga, ON, Canada) at a sampling rate of 500 Hz. The eye-tracker was calibrated with a default nine-point grid at the beginning of the experiment, which was repeated if necessary during the experiment. Saccades and blinks were detected with the built-in event detection, which classified onset and offset of a saccade when the thresholds of 30°/s velocity and 8,000°/s^2 acceleration were exceeded and subceeded. Blink onset and offset were defined by loss and recovery of pupil.

EOG.

For EOG data acquisition we used a Biosemi Active Two EEG system (Biosemi Instrumentation, Amsterdam, The Netherlands) but only collected data from eight external electrodes placed around the eyes to allow for binocular EOG recordings (Fig. 1*A*). Electrodes were combined into horizontal and vertical channels for each eye. We subtracted the lower from the upper electrode signal to form the vertical EOG channel and the left from the right electrode signal for the horizontal EOG channel of each eye. All data were recorded at 2,048 Hz and preprocessed with a Savitzky–Golay filter of second order and time frame of 25 ms (24). EOG and EyeLink data were coregistered with TTL triggers sent simultaneously to both devices.

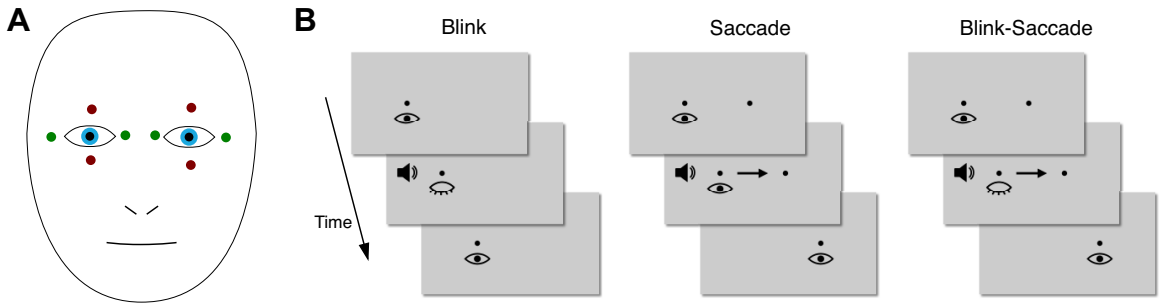

Figure 1. Electrode placement (*A*) and experimental protocol (*B*). *A*: 4 electrodes were placed around each eye. The difference between upper and lower electrode (red) formed the vertical channel, whereas the difference between right and left electrode (green) formed the horizontal channel. *B*: participants performed 1 of 3 tasks. In the Blink task, participants had to blink as soon as they heard an auditory cue. For the Saccade task, they had to shift their gaze to a target dot after an auditory cue. The third task was a Blink-Saccade combination, where participants were instructed to shift their gaze shift while blinking.

Dynamic magnetic resonance imaging.

For independent verification of crucial aspects of the results from EOG data, we invited two of the participants for an additional experimental session using high-speed magnetic resonance imaging (MRI). A 3-T Philips Achieva scanner (Philips Medical Systems, Best, The Netherlands) was used for examination, with instructions and visual stimuli displayed with a back-projection monitor. Initially, a three-dimensional (3-D) T2-weighted MR sequence was acquired [matrix = 256 × 256 × 250, field of view (FOV) = 250 × 250 × 250 mm, voxel size = 0.98 × 0.98 × 1.00 mm, echo time (TE) = 225 ms, repetition time (TR) = 2,500 ms, slice thickness = 2 mm, flip angle = 90°, scan duration = 232.5 s] while participants fixated a dot at the center of the screen. On the basis of this anatomical scan we chose an appropriate slice position to capture eyeball motion in the axial plane. A balanced steady-state free precession (bSSFP) sequence enabled us to acquire single-slice data at a temporal resolution of 55.6 ms (matrix = 224 × 224, FOV = 200 × 200, voxel size = 0.89 × 0.89 mm, TE = 1.28 ms, TR = 2.56 ms, slice thickness = 3 mm, flip angle = 45°, 1,020 dynamic scans, total scan duration = 56.7 s, K-t BLAST factor of 5). Eye kinematics in terms of horizontal gaze and eyeball retraction were quantified with MREyeTrack (4), which provides a segmentation of sclera, lens, and cornea for each image. For further analysis, we upsampled the eye motion data with linear interpolation to a 2-ms time interval and then smoothed it with a Savitzky–Golay filter of second order with a window of 100 ms.

Experimental Protocol

Our study consisted of three experimental tasks: Blink, Saccade, and Blink-Saccade (Fig. 1*B*). Across one session, participants had to perform 80 Saccade trials, 80 Blink-Saccade trials, and 120 Blink trials. The Blink trials were split into 60 trials before and after the Blink-Saccade block in case of changes in blinking behavior. Half of the participants performed the Blink-Saccade block before the Saccade block; the others performed the Saccade block first. Before the start of the actual experiment, the EyeLink had to be calibrated and participants performed a few practice trials of each task.

Blink.

Participants fixated a dot at (−2.5°, 0°) on the screen for a randomized duration between 500 and 1,000 ms. The video-based eye-tracker was used to ensure that gaze was within a 2° radius of the dot for the fixation period. If fixation was broken, the trial was repeated. After the fixation period, we presented an auditory cue in response to which participants had to blink. Participants were instructed to aim for a short and soft blink. The fixation dot remained visible for 500 ms after blink offset before it disappeared, signaling the end of the trial.

Saccade.

Similar to the Blink task, each trial started with a fixation period between 500 and 1000 ms while presenting a fixation dot at (−2.5°, 0°). Instead of a blink, participants now had to make a saccade to a target dot (2.5°, 0°) as soon as they heard the auditory cue. In one of the two sessions, the target dot was visible during the fixation period, so that the saccade was visually guided. In the other session, that target dot was shown only after the saccade was already executed. Therefore, saccade execution relied on memory of target position that was building up over consecutive trials. We used these two different saccade types because visually guided and memory-guided saccades were shown to have slightly different kinematics in an earlier blink study by Powers et al. (25). In our data, however, the kinematics were not different (likely because we measured 5° saccades whereas Powers et al. investigated saccades in the 10–20° range), so we pooled the data for our analysis.

Blink-Saccade.

The experimental protocol was identical to the Saccade task, but this time participants were instructed to perform the saccade while blinking. Even though participants were initially unsure about whether they would be able to perform this task, data showed that all participants performed it without problems during the experiment.

Data Analysis

Baseline drift estimation.

The EOG signal measures eye movements but is also affected by various sources of noise such as background signal interference, varying electrode contact pressure, or changes in skin resistance due to sweating. These noise sources typically produce a low-frequency drift of the EOG (22). Eye movements such as saccades typically only last a

few dozen milliseconds and thus operate on a timescale different from the relatively slow baseline drift (Fig. 2*A*). We used the simultaneously collected EyeLink data to estimate the baseline drift in EOG data. This way, we could clearly distinguish whether changes in EOG voltage were caused by gaze changes or the baseline drift. First, we collected saccade onset and offset from all regular saccades recorded by the EyeLink across one recording session. This also included saccades not related to the experimental task or those that happened during breaks. Then, we compared the EyeLink saccade amplitude to the voltage difference in horizontal EOG channel data at the respective time (Fig. 2*B*). Linear regression analysis between EyeLink and EOG saccade amplitude yielded highly significant correlation between the two data sources (Pearson's r was at least 0.91 and $P < 0.001$ for each session of each participant). We used the linear model to subtract eye movement traces from the EOG channels and fitted the remaining signal (assumed to be the baseline drift) with a fifth-order polynomial (Fig. 2*C*). For trials containing blinks, we excluded EyeLink data from 50 ms before blink onset to 100 ms after blink offset and only then performed the polynomial fit. This way, the baseline drift signal could be estimated even in the temporary absence of valid EyeLink data. Finally, the estimated baseline drift signal was subtracted from the original EOG signal, and horizontal EOG channel data were transformed from voltage to degree. Example results of this procedure can be seen in Fig. 2*D*.

Blink signal removal.

Our goal was to extract the saccade kinematics from the horizontal EOG channel data. During within-blink saccades, the horizontal EOG channel picks up signals from the saccadic gaze shift, the blink-related eye movement, and further components related to the lid movement. All blink-related components need to be subtracted in order to analyze the saccadic trajectory. A simple approach would be to average across blink trials with negligible gaze shift and subtract this averaged template from the trials with gaze shifts to extract the saccade kinematics (13). This led to unsatisfactory results for some participants, however, likely because they had large variability in blink duration and lid movement amplitude. Both of these sources of variability are well captured by the vertical EOG channel, which is in turn not affected by any horizontal gaze shift signal. Additionally, it has been shown that eyelid deviation is predictive of initial eye excursion during the BREM (21). Therefore, we designed a procedure that predicts the blink signal in the horizontal channel based on the respective vertical channel signal (Fig. 3). First, we pick the horizontal EOG channel for trials with negligible gaze shift and perform a principal component analysis (PCA) on them. Only the three largest components are kept, such that each trial is parametrized by the three respective coefficients. Three components were necessary to capture the variance of the EOG blink signals, but adding further components did not seem to improve the analysis and rather led to overfitting. The same procedure of

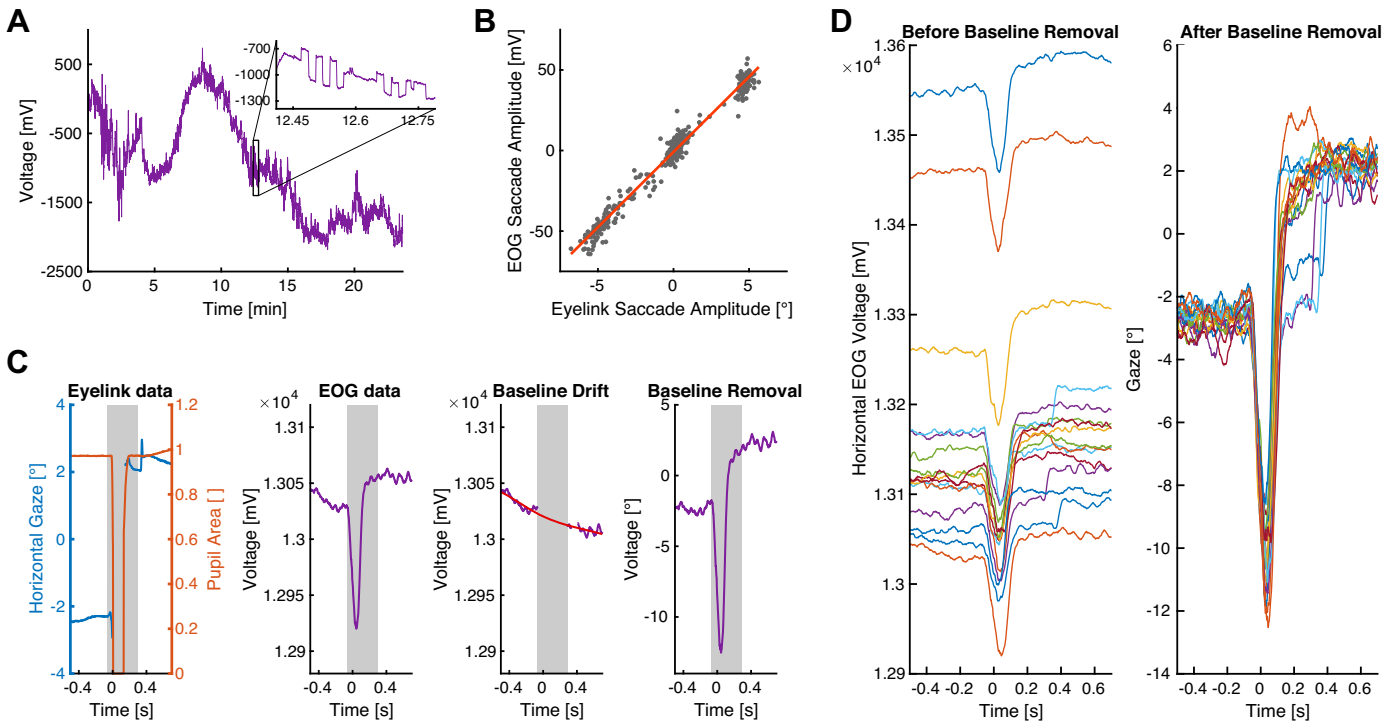

Figure 2. Baseline drift removal. *A*: horizontal electrooculography (EOG) channel over the time course of a full session. Even though short-term gaze changes are well reflected by the data on a smaller scale, the overall baseline drift makes the interpretation of gaze data difficult. *B*: comparison of saccade amplitude measured by EyeLink and EOG. Linear regression fit in red. *C*: illustration of the baseline drift removal process. EyeLink pupil area data are used to define a time window where the EyeLink data are deemed unreliable. Reliable EyeLink gaze data are then subtracted from the horizontal channel EOG data. The remaining signal is fitted with a 5th-order polynomial to estimate the baseline drift. Finally, the estimated baseline drift is subtracted from the EOG data. *D*: 16 example trials from the Blink-Saccade task before and after removal of the baseline drift. Data from right eye of *participant P1*.

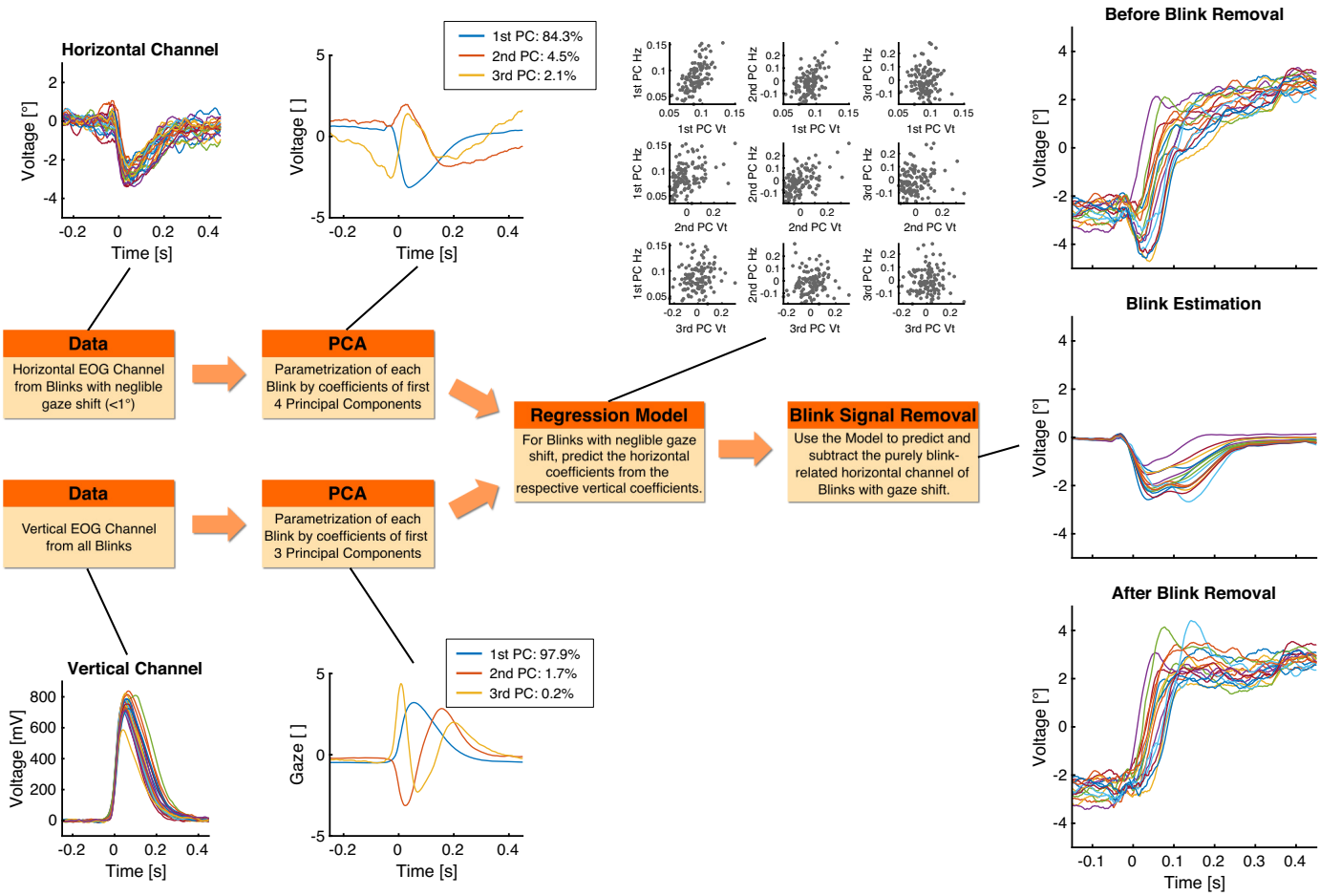

Figure 3. Illustration of the blink removal process. The trajectories of saccades that coincide with blinks are recovered by estimating and subtracting the purely blink-related component of the horizontal electrooculography (EOG) channel data. Estimation of the blink component is performed on the subset of blinks with negligible gaze shift. We start by independently parametrizing the horizontal and vertical EOG channel data by the three largest principal components (PCs) of the respective principal component analysis (PCA). A multilinear regression model is then trained to predict the horizontal from the vertical components. The model is finally applied to Blink-Saccade trials, such that the estimated blink component is subtracted and the saccade trajectory recovered. Data from *participant P1*.

performing a PCA and keeping the three largest components is applied to the respective vertical EOG channel trials. Next, we run a multiple linear regression model to predict the horizontal channel coefficients based on the vertical channel coefficients. After having trained the regression model on Blink trials with negligible gaze shift, we applied it to Blink-Saccade trials. Based on the PCA coefficients of the vertical EOG channel, we used the regression model to predict the blink-related signal of the horizontal EOG channel for each individual Blink-Saccade trial. These estimated blink signals were then subtracted from the horizontal EOG channel data, so that only the saccadic gaze shift signals remained. Note that we made no further attempt to separate the blink-related signal into eye and lid movement components.

We tested the performance of this procedure against the simple approach of subtracting an averaged blink template. Eighty percent of Blink trials were defined to be the training set, and the remaining 20% made up the testing set. We trained each procedure on the training set and tested the performance by calculating the least squared error per sample between prediction and test set data. Both methods led to similar results for most participants, but for some participants the regression model led to substantial improvements (Table 1).

Saccade detection in EOG data.

For saccade detection in the horizontal EOG channel data, we used the same velocity and acceleration thresholds (30°/s and 8,000°/s^2) as for the EyeLink data. Furthermore, we required the saccade candidates to surpass these thresholds for at least 10 consecutive milliseconds and to have a minimum amplitude of 1°. We found many saccades with large dynamic overshoots during the Blink-Saccade task (see Fig. 6). These saccades briefly stopped when reaching their maximum excursion, but the movement continued almost immediately in the reverse direction. Saccade offset was therefore determined when velocity and acceleration fell below the thresholds and also stayed below them for the subsequent 50 ms. Saccades with dynamic overshoot are not fully described by the conventional metrics of amplitude, duration, and peak velocity, which is why we additionally kept track of the maximum excursion relative to saccade

Table 1. *Comparison of our blink model removal procedure with subtraction of an averaged blink template*

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Session 1	−0.40	−0.03	−0.01	−0.02	−0.02	0.01	−0.01	−0.04	−0.15	0.00	−0.16	−0.14
Session 2	−0.80	−0.02	0.02	−0.03	0.01	0.01	−0.01	0.00	−0.03	−0.21	−0.06	−0.08

Values are difference in least squared error per sample for *participants P1* through *P12*.

onset. Saccade amplitude on the other hand was defined as the difference in gaze between onset and offset. For saccades without a dynamic overshoot, the metrics of amplitude and maximum excursion are identical. Furthermore, we kept track of the overshoot size, which was defined as the difference between maximum excursion and amplitude.

Blink detection in EOG data.

Episodes of pupil loss by the EyeLink were used to coarsely locate blinks in the EOG data time course. Then, to detect onset and offset of blinks more precisely, we applied a velocity threshold algorithm to the vertical EOG channel data of each participant. Blinks manifest themselves as sharp, Gaussian-like peaks in the vertical EOG channel. Since the respective EOG amplitudes were highly variable across participants, blink onset and offset thresholds were defined as 5 and 3 median absolute deviations from all velocity data for each participant. The EOG velocity profile is characterized by a positive peak related to lid closure and a negative peak related to lid opening. Blink onset was determined by finding the first sample below onset threshold before the positive EOG peak. Likewise, blink offset was determined by identifying the first sample above offset threshold after the negative EOG peak.

Trial selection criteria.

We disregarded trials in which participants executed the wrong task (saccade instead of blink and vice versa), made excessively long blinks of >500 ms, or made double blinks. Additionally, we excluded Blink trials when they were accompanied by a gaze shift of >1°.

RESULTS

Comparison of Blink Measurements between EyeLink and EOG

The simultaneous measurement of the lid movement by the vertical EOG channel and the pupil area by the video-based eye-tracker allows the comparison of two different aspects of blinks: the lid movement, as measured by EOG, and the resulting loss of vision, as measured by EyeLink pupil area (Fig. 4). We compared EOG and EyeLink measures of blink onset. Whereas EOG blink onset relates to the shunting of the corneo-retinal potential as the eyelid starts moving

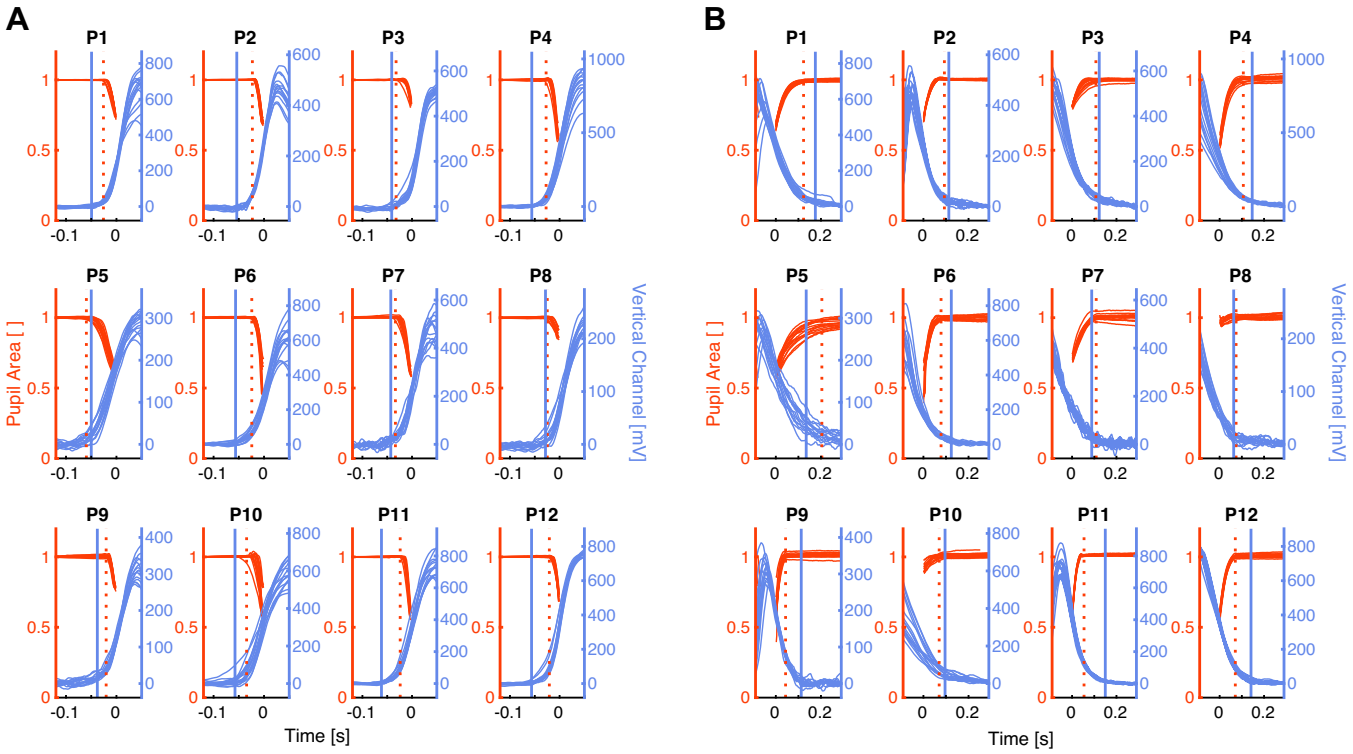

Figure 4. Comparison of EyeLink pupil area and vertical electrooculography (EOG) channel. *A*: pupil area (red) and vertical EOG channel (blue) for each participant (*P1* through *P12*) aligned to loss of pupil by the EyeLink. Pupil area is normalized to 1 for each trial. Blue (solid) and red (dashed) vertical lines indicate EOG and EyeLink onset. *B*: same data but aligned to recovery of pupil by EyeLink. Blue (solid) and red (dashed) vertical lines indicate EOG and EyeLink offset.

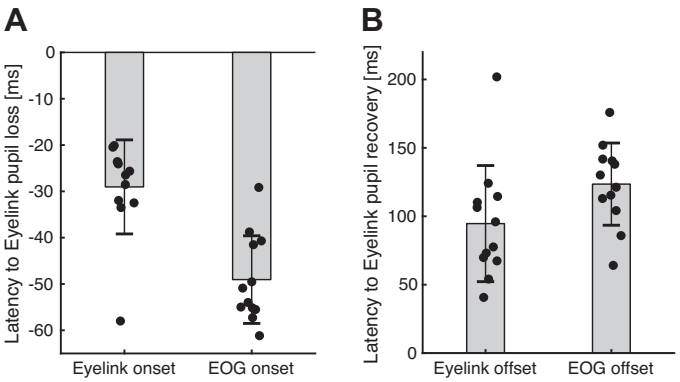

Figure 5. Blink onset and offset relative to vision recovery and loss. *A*: averaged latency of blink onset measured with electrooculography (EOG) and EyeLink relative to loss of pupil by EyeLink for each participant. Error bars are SD. *B*: same for EyeLink and EOG offset relative to EyeLink pupil recovery.

across the cornea, EyeLink blink onset relates to the initial decrease in pupil area, which is expected to lag behind EOG onset by a few milliseconds. Furthermore, EyeLink pupil area measurements provided us with the time of pupil loss, which we took as a proxy for loss of vision. Typically, the EyeLink lost track of the pupil when its area had decreased by 30–50%, but this varied considerably across participants (Fig. 4*A*). EOG onset of blink occurred 49 ms (SD = 10 ms) and EyeLink onset 30 ms (SD = 12 ms) before loss of pupil (Fig. 5*A*). Similarly, we compared EOG and EyeLink offset of blink with recovery of pupil by EyeLink and found that EOG offset occurred 123 ms (SD = 33 ms) and EyeLink offset 116 ms (SD = 59 ms) after recovery of pupil (Fig. 5*B*). However, pupil area after a blink may not reflect the increase in pupil size due to the upward-moving lid alone but also actual changes in pupil size due to changing light conditions. For these reasons, EOG recordings of lid movement seem to be a more reliable measure of blink onset and offset compared with measurements based on EyeLink pupil area, in particular when comparing measures across different participants. For the rest of this report, onset and offset of blink refer to onset and offset of lid movement as measured by the vertical EOG channel, unless otherwise indicated.

Dynamic Overshoot of Within-Blink Saccades

A notable feature of the within-blink saccades data was the occurrence of large dynamic overshoots for some trials (Fig. 6). These overshoots occurred in both experimental sessions, with no noticeable difference between saccade types. In fact, we found no differences throughout our analysis of overshoots, kinematics, and temporal coupling of saccades with blinks, which is why we pooled the data for all reported analysis. Overshoots were observed in all participants, but size and frequency varied widely across participants. For further analysis, we ordered participants by the average size of overshoot from lowest to highest (Table 2). Average size of overshoot and frequency of occurrence were positively correlated (P = 0.001). Although some participants (like *P1*, *P2*, and *P4*) had only very few occurrences, the size of those overshoots (~2°) is quite large for a 5° saccade and far exceeds the subtle dynamic overshoots that can accompany saccades without blinks (26). *P11* and *P12*, on the other end of the scale, made overshoots in around two-thirds of all within-blink saccades by an average amount of 5.4° and 10.5°, respectively. Dynamic overshoots of within-blink saccades have been reported in an earlier study by Rottach et al. (20), but they observed only a 1–2° overshoot for a 20° saccade. The overshoots of *P12*, on the other hand, were on average twice as big as the actual saccade amplitude. To check that the EOG signal of *P12* truly represented the saccade trajectory and not, for example, the blink-related eye movement, we looked at the horizontal EOG channel signal before blink removal for both eyes (Fig. 7). The massive overshoot is present in both eyes and crucially has the same polarity. If the overshoot signal should have originated from the blink-related eye movement, one would have expected opposite polarity between left and right eye data. Moreover, the

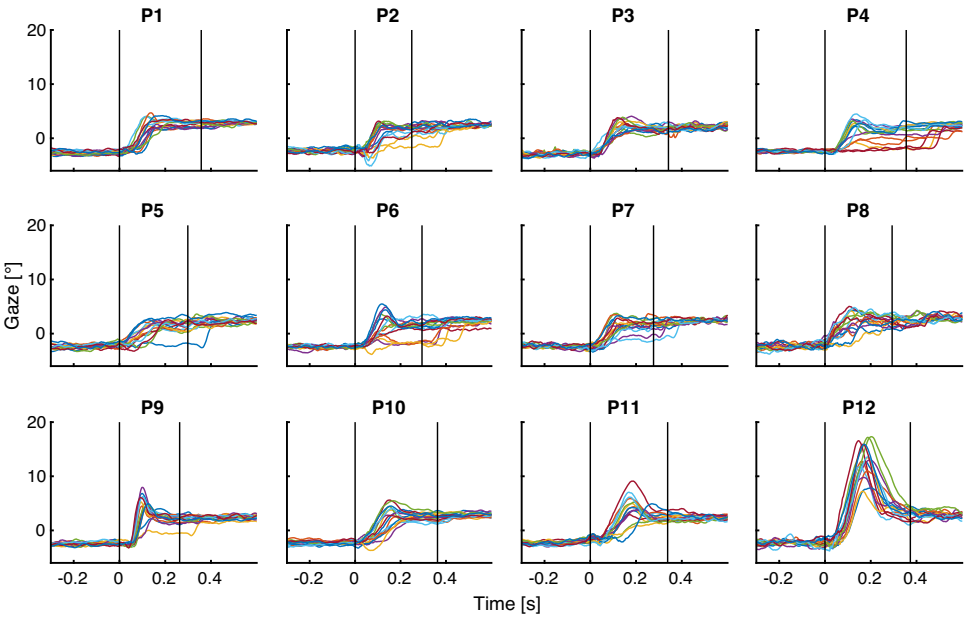

Figure 6. Trajectories of within-blink saccades. We randomly picked 15 Blink-Saccade trials of each participant. Participant numbers (*P1* through *P12*) are sorted in increasing order of average overshoot size. Whereas the *top* row of participants shows saccades with normal but slower than usual trajectory, participants in the *middle* and *bottom* rows exhibit large overshoots far exceeding the actual saccade amplitudes (in particular *P12*). Note that some participants (in particular *P4*) failed to saccade while blinking in a few trials and reached the target through a catch-up saccade after the blink.

Table 2. *Average size and frequency of within-blink saccade overshoots*

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Size, °	1.6	1.7	2.1	2.2	2.3	3.0	3.0	3.1	3.2	3.3	5.4	10.5
Frequency, %	1.2	2.7	11.3	10.7	3.9	18.1	11.7	16.6	44.8	18.6	70.5	64.2

P1–P12, participants P1 through *P12*.

horizontal EOG channel showed no strong excursions for trials of blinks without gaze shift, further confirming that the overshoot was not related to other eye movements during blinks.

Independent Verification of Dynamic Overshoots by Dynamic MRI

To further confirm that these dynamic overshoots truly represent movement of the eye and are not caused by some unwanted source of corruption in the EOG data, we decided to repeat some of the measurements with another recording technique. Our laboratory recently developed MREyeTrack (4), a novel eye-tracking method based on high-speed magnetic resonance imaging (MRI). This produces many fast measurements of an entire cross section of the eye, which allows eye-tracking even while the eye is closed and also takes displacements of the whole eyeball into account. It is therefore particularly well suited to measuring eye movements during blinks and allows the reader to convince themselves from the raw video footage that dynamic overshoots of the reported size really occur during blinks. We invited *participants P9* and *P12*, who were among those with the largest overshoots, for an additional recording session of 5° within-blink saccades. Dynamic overshoots of within-blink saccades were clearly visible in both eyes of both participants, and their eye kinematics were analyzed with MREyeTrack. For *participant P12*, the dynamic overshoots had an average size of 6.3° (SD = 2.5°) and could even reach >10° (Fig. 8*B* and Supplemental Movie S1; available at https://doi.org/10.6084/m9.figshare.19525441). Dynamic overshoots of *participant P9* were smaller and had an average size of 3.1° (SD = 1.4°) (Fig. 8*A* and Supplemental Movie S2; available at https://doi.org/10.6084/m9.figshare.19525450). These results are in good agreement with those obtained from the analysis of EOG gaze data and further confirm the validity of the EOG data analysis. The MRI data have the additional advantage of simultaneously measuring eyeball retraction during within-blink saccades. Close inspection of both of the Supplemental Movies shows that the dynamic overshoots are closely time-locked to eyeball retraction. This is particularly noticeable in the data of *participant P12*, who made two blinks of longer than usual duration (blue and red traces in Fig. 8*B, right*). The respective gaze trajectories (Fig. 8*B, center*) show that these two within-blink saccades not only had a strong dynamic overshoot but also held out at maximum excursion as long as the eye was fully retracted.

Kinematics of Within-Blink and Without-Blink Saccades

Saccade kinematics are highly stereotyped and show strong consistent relationships between amplitude, peak velocity, and duration, coined the main sequence (27). We plot amplitude against peak velocity for both without-blink and within-blink saccades in Fig. 9*A*. Although without-blink saccades exhibit a clear linear relationship between amplitude and peak velocity (as expected for saccades in that range), this was not the case for within-blink saccades. In

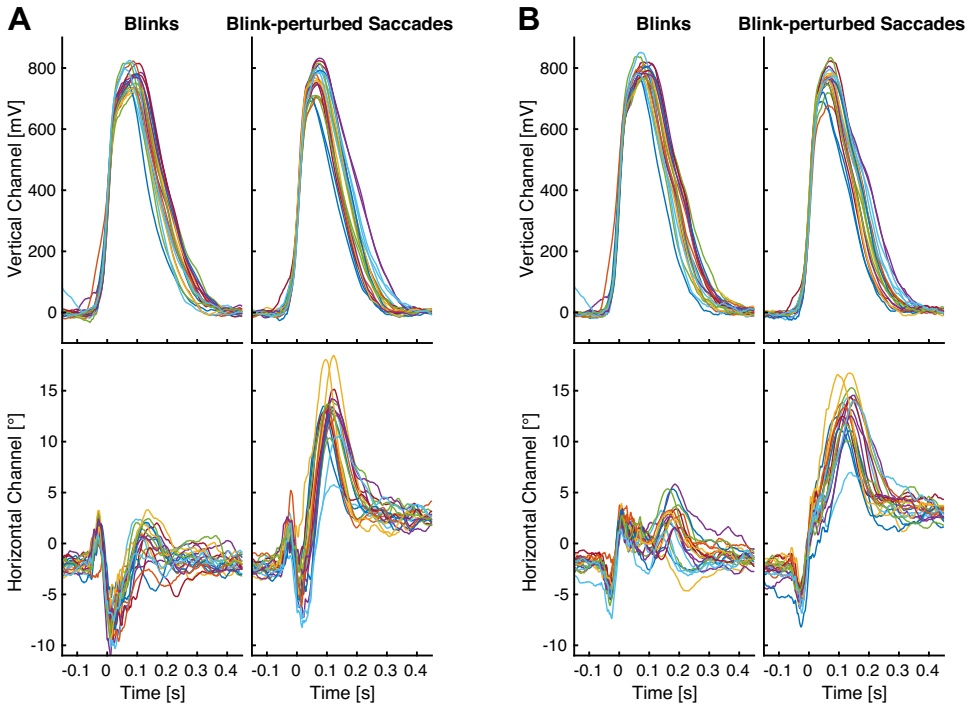

Figure 7. Binocular recordings of within-blink saccade overshoots. Twenty example trajectories of horizontal and vertical electrooculography (EOG) channel data during Blink and Blink-Saccade task for the left (*A*) and right (*B*) eye. The presented data have the baseline drift removed, but the blink signal was not yet subtracted from the horizontal channel. Overshoots are clearly visible during the Blink-Saccade task in the *bottom right* panel for each eye. Note that the initial excursion in the horizontal channel is in opposite directions when comparing right and left eye but saccade and overshoot direction are in the same direction. Vertical channel data differ only slightly between Blink and Blink-Saccade trials, and there is barely any discrepancy at all between right and left eye data.

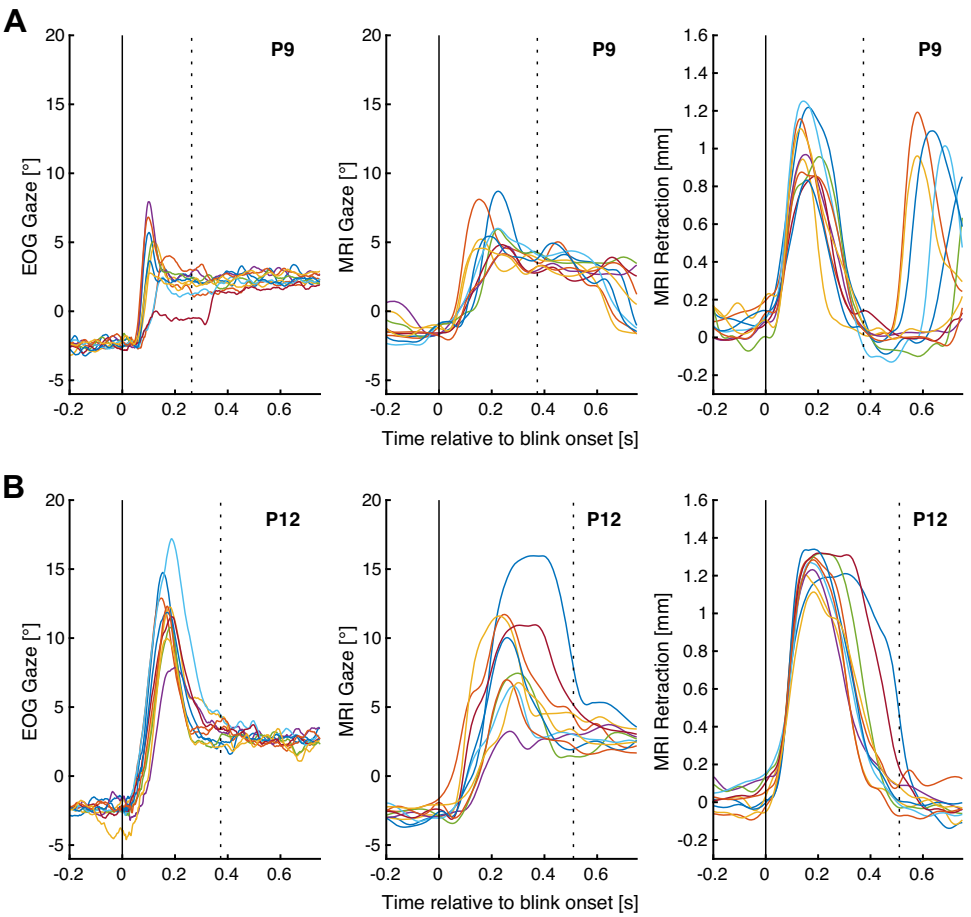

Figure 8. Comparison of eye kinematics during within-blink saccades of *participants P9* (*A*) and *P12* (*B*) measured with electrooculography (EOG) and dynamic MRI. The panels show 10 example trajectories of gaze and retraction from the respective recording technique and participant. Vertical lines are at blink onset (solid line) and averaged blink offset (dotted line). Note that the EOG data were recorded at a sampling rate of 2,000 Hz and the MRI data at a sampling rate of roughly 20 Hz. Therefore, high-frequency components are more pronounced in the EOG gaze data, which results in sightly sharper and higher peaks compared with the MRI gaze data. EOG data (*left*) and MRI data (*center* and *right*) were recorded in different sessions and therefore do not show identical trials. We still obtained the same temporal characteristics, the time-locking to blink onset, and crucially also a similar amount of dynamic overshoot.

particular, participants with a frequent occurrence of overshoots like *P9*, *P11*, and *P12* seemed to lack any relationship between amplitude and peak velocity. The picture changed when we used maximum excursion during the saccade instead of amplitude. For saccades with dynamic overshoot, maximum excursion is larger than final saccade amplitude. Participants with frequent overshoots showed a linear relationship with peak velocity when maximum excursion instead of amplitude was considered (Fig. 9*B*).

The slope of the linear relationship between maximum excursion and peak velocity was lower for within-blink saccades compared with those without blinks for all participants. This is not surprising, since reduced peak velocity has been described as the main feature of within-blink saccades in various studies (18, 20, 21). However, we also found that the slopes of without-blink and within-blink saccades were tightly correlated (P = 0.002). As depicted in Fig. 10, participants with slower without-blink saccades had proportionally slower within-blink saccades. The three participants with the biggest overshoots (*P10*, *P11*, and *P12*) had the lowest slope of the within-blink saccade data.

Temporal Effects of Blinks on Saccade Metrics

Finally, we looked at the timing of all saccades in a time window of 300 ms before and 700 ms after blink onset (Fig. 11). We found tight temporal coupling between blink onset and saccade onset for every single participant. Such a tight temporal coupling has been reported before for reflex blinks (13, 17), and the same seems to hold true for voluntary blinks in our data. Across all participants, almost all of the onsets of saccades that overlapped with blinks fell in a narrow time window of 0 and 100 ms after blink onset, as can be seen in Fig. 12*A*. Reversely, we found only 18 out of a total 1,524 saccades across all participants were initiated in the 100 ms preceding blink offset (Fig. 12*A*). Relative to blink onset as determined by EOG, many saccades were initiated directly after blink offset. We wondered whether these were corrective saccades due to postsaccadic visual error. Therefore, we also looked at saccade onset relative to loss and recovery of vision as determined by the video-based eye-tracker (Fig. 12*B*). Indeed, the saccades after blink offset were initiated at least 100 ms after recovery of vision, which is in line with typical saccade reaction times. Apart from the tight temporal coupling between blink onset and saccade onset, there was also a strong relationship between the time of maximum lid excursion and the time of maximum eye excursion (Fig. 13). We performed a linear regression analysis and obtained a Pearson's r between 0.25 and 0.74 for each participant.

DISCUSSION

We used EOG to measure the timing and kinematics of horizontal within-blink saccades and compared them to saccades without blinks. Developing a model to predict the exclusively blink-related components based on the vertical

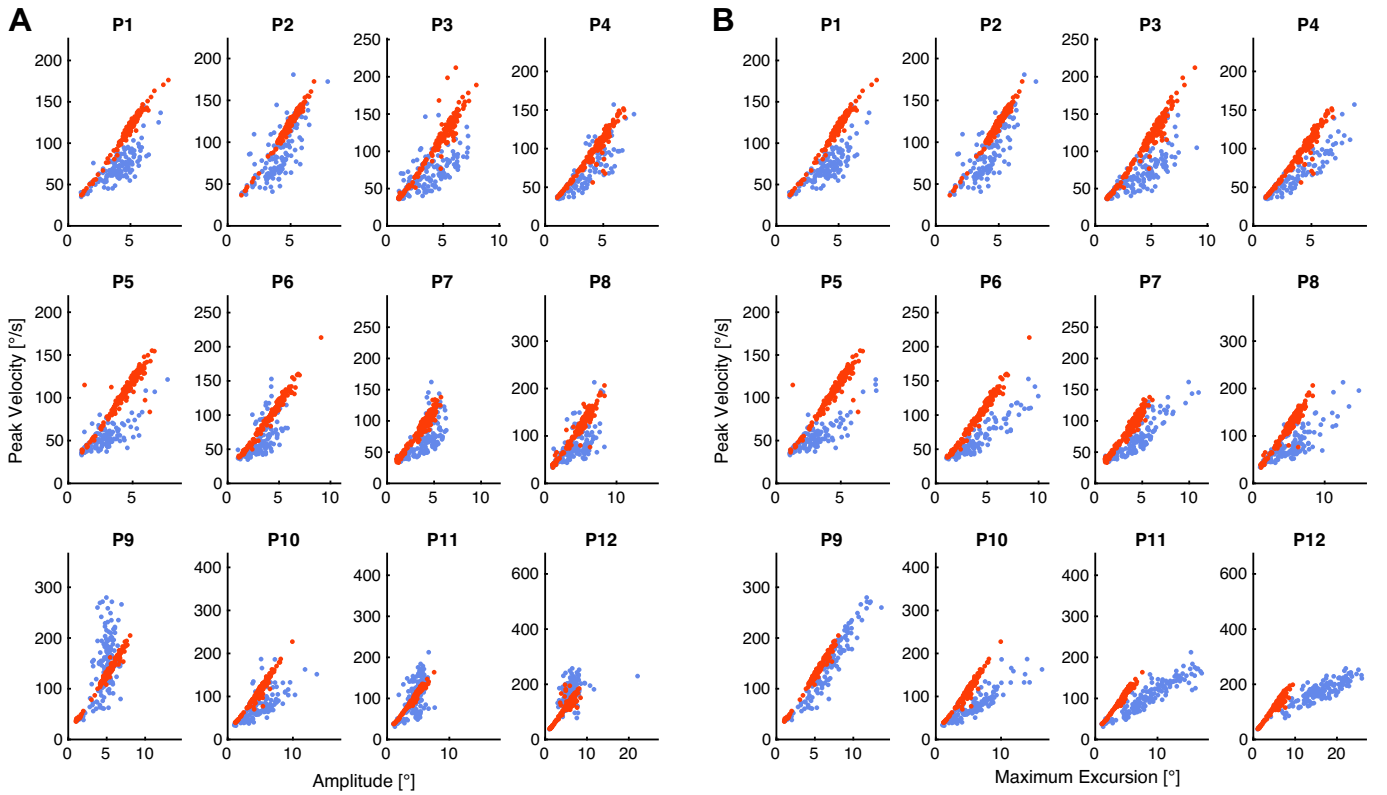

Figure 9. Saccade main sequence analysis. *A*: peak velocity of each saccade plotted against the respective amplitude for without-blink saccades (red) and within-blink saccades (blue). The without-blink saccades follow the linear relationship of the main sequence, as expected for saccades in that range of amplitudes. A similar linear relationship for within-blink saccades exists only for the participants with little overshoot in the *top* rows. *B*: maximum excursion, instead of amplitude, plotted against peak velocity for without-blink saccades (red) and within-blink saccades (blue). Both saccade types show a linear relationship between maximum excursion and peak velocity for every single participant. *P1–P12, participants P1* through *P12*.

EOG channel allowed us to extract the saccadic gaze shift. The main finding of this study was the frequent observation of large dynamic overshoots in within-blink saccades, for one participant even twice the size of the actual saccadic amplitude. This finding was independently confirmed by dynamic MRI measurements. Within-blink saccades with dynamic overshoot did not exhibit the typical linear relationship between amplitude and peak velocity (27); instead they showed such a relationship only when considering maximum excursion instead of amplitude. In agreement with previous studies, we found that within-blink saccades had strongly reduced peak velocities compared with saccades without blinks and exhibited tight temporal coupling between blink and saccade onset. Beyond that, we also found that the time of maximum lid excursion was positively correlated with the time of maximum saccade excursion. Our results show that the combined eye movement during blinks cannot be described as a simple superposition of a BREM and an unusually slow saccade but there must be additional interference with saccade execution leading to dynamic overshoots.

Dynamic overshoots could be caused by inhibition of omnipause neurons (OPNs) during blinks, the simultaneous cocontraction of extraocular muscles, or a combination of both. The onset of a BREM is quickly followed by inhibition of OPNs, which in turn causes an impending saccade to be initiated early. This is reflected by the tight coupling of saccade onset with the onset of reflex blinks (17) and of voluntary blinks in our data. Our observation that most saccade onsets preceded the lid covering of the pupil and the associated loss of vision (Fig. 12*B*) further supports the hypothesis that the temporal coupling is due to physiological constraints. Our data also showed that saccades, if they occurred within a blink, were always initiated directly after blink onset. We found barely any saccades initiated in the second half of the blink, as illustrated by the gap of saccade onsets for the 100 ms preceding blink offset in Fig. 12*A*.

Our results appear to be in disagreement with those of Rambold et al. (18), who did not observe such a tight temporal coupling between saccade and blink onset as we did. A possible reason for this could be differences in the experimental protocol. Since blink and saccade had to be prepared and initiated only when participants heard an auditory cue in our study, this could have resulted in stronger temporal coupling between blink and saccade. However, data in Fig. 4 of the Rambold et al. paper suggest that there is a gap of almost 100 ms between saccade onsets within blink and saccade onsets after blink. We also observed such a gap in the 100 ms preceding blink offset (Fig. 12*A*). The wider distributions of saccade onsets relative to blink onset reported by Rambold et al. might furthermore be explained by the fact that Rambold et al. did not subtract the BREM from the within-blink saccadic

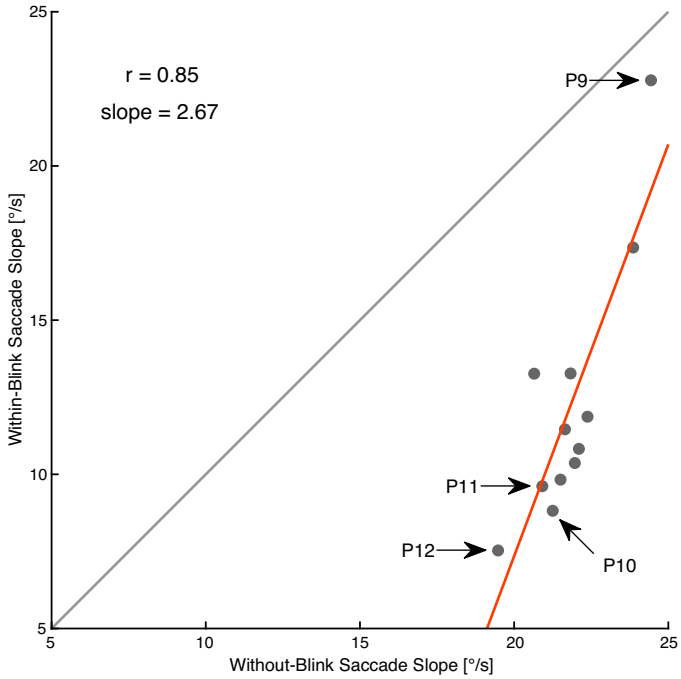

Figure 10. Slope of saccade main sequence. Slope of main sequence (excursion vs. peak velocity) for without-blink saccades plotted against the slope for within-blink saccades. We performed a linear regression analysis on the data and found that the slopes were highly correlated (P = 0.002). *P9–P12, participants P9* through *P12*.

gaze shift. They determined saccade onset when velocity exceeded 5% of the peak velocity of the superimposed BREM and saccade. Subtraction of the blink-related eye movement and subsequent calculation of saccade onset could lead to a saccade onset distribution more similar to ours.

Given the excessive size of dynamic saccade overshoots observed in our experiments, it is strange that they have barely been reported in earlier studies. To our best knowledge, the only other study that reported at least small dynamic overshoots in relation to within-blink saccades was by Rottach et al. (20). We think that three factors might have prevented earlier studies from registering large overshoots. First, dynamic overshoots may occur more frequently for saccades of relatively small amplitude. Most studies on within-blink saccade in humans focused on saccades of 20° or more (18, 20, 21), probably because blinks are more likely to go along with large gaze shifts (28). In fact, Rottach et al. reported that dynamic overshoots were observed more often with saccades of 20° amplitude than with those of 40° amplitude. Second, our data suggest that size and occurrence of dynamic overshoots vary widely across individual participants, as opposed to other features of within-blink saccades like tight temporal coupling. Monkey studies or scleral search coil studies on human participants rarely exceed the number of five participants, such that individual differences might have been missed. Third, no former study systematically subtracted the BREM contribution from the superimposed eye movement that occurs during blinks. Dynamic overshoots that might have occurred could have been attributed to the BREM instead of the saccadic gaze shift.

Dynamic overshoots challenge the hypothesis that the combined eye movement during blinks can be understood as a superposition of BREM and a slow but straight saccade (13, 21). What could be the cause of these dynamic overshoots? Zee and Robinson (29) described a patient with neurological disorder, who exhibited similar behavior when executing saccades without blinks. They proposed a model of the saccade premotor circuit that linked dynamic overshoots to a failure of the OPN to properly resume discharging at the end of saccades. Rottach et al. also favored

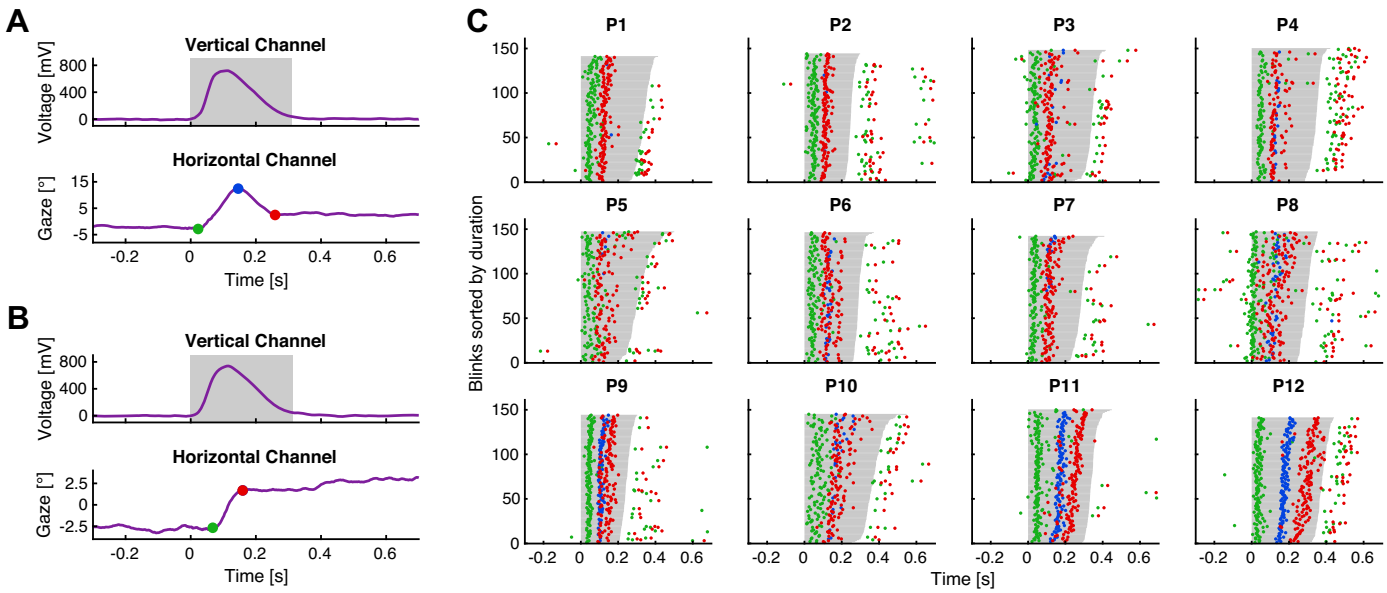

Figure 11. Saccade timing. *A*: example of a within-blink saccade with large overshoot. Blink duration is illustrated by a gray background in the vertical channel, and markers in the horizontal channel indicate saccade onset (green), offset (red), and excursion (blue). *B*: example of a within-blink saccade without overshoot. Same as *A* but without the overshoot marker. *C*: saccade onset (green), offset (red), and, if applicable, overshoot (blue) of each saccade from all valid Blink-Saccade trials. Blink duration of each trial is represented as shading in gray. *P1–P12, participants P1* through *P12*.

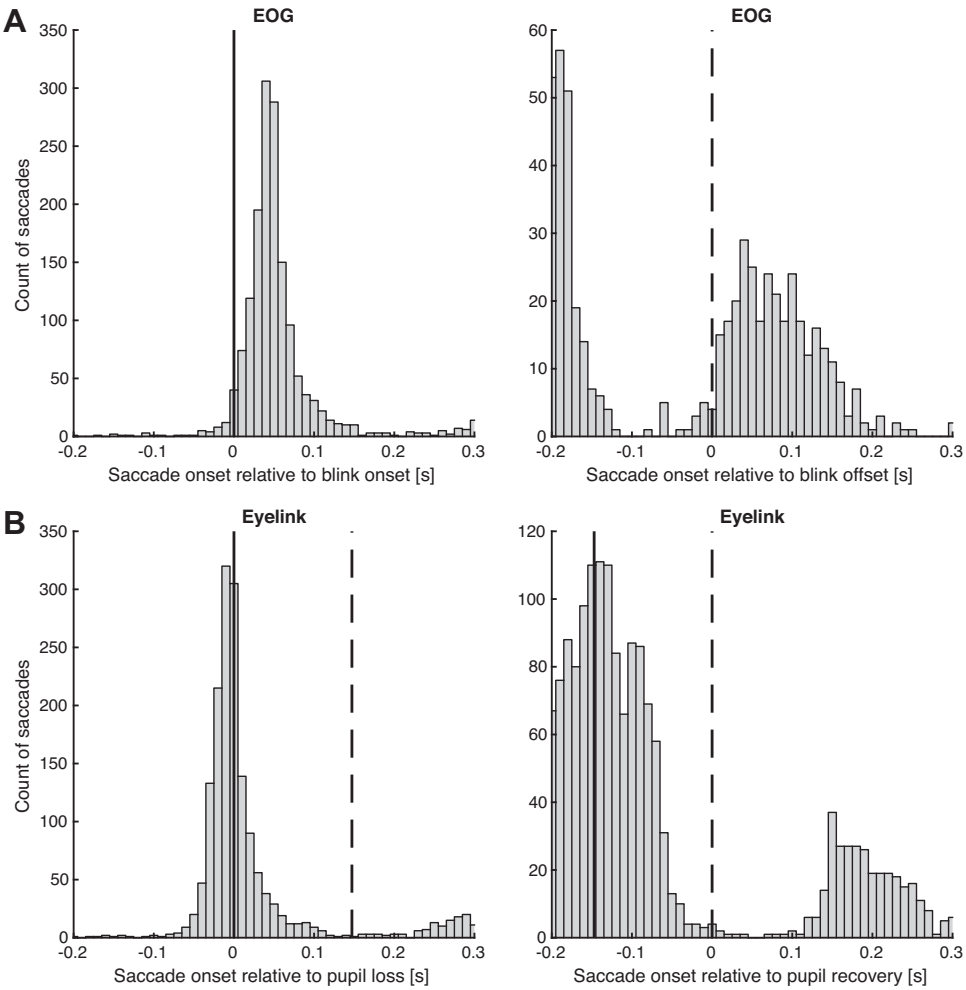

Figure 12. Saccade onset relative to blink timing. *A*: histogram of saccade onsets pooled from all participants relative to blink onset and offset as determined by the vertical electrooculography (EOG) channel. Bin width, 10 ms. Note the narrow peak relative to blink onset and the almost complete lack of onsets in the 100 ms preceding blink offset. Averaged blink onset shown by solid line and average blink offset by dashed line. *B*: same as *A* but aligned to loss and recovery of vision as determined by EyeLink pupil area. Note that saccades were typically initiated before loss of vision and catch-up saccades started to occur 100 ms after recovery of vision. Average time of pupil loss is shown by solid lines and averaged pupil recovery by dashed lines.

this hypothesis, because it would explain why dynamic overshoots are more likely to go along with saccades of smaller amplitude. If the pulse duration of saccades is shorter than the duration of OPN inhibition during blinks, this might result in dynamic overshoots of the saccades. The observed link between time of maximum lid excursion and time of maximum saccade excursion seems to support the idea that dynamic overshoots could be caused by prolonged inhibition of the OPN. However, we did not observe a clear link between blink duration and dynamic overshoot occurrence (Fig. 11), and participants with strong overshoots (*P10*, *P11*, and *P12*) were also those with the slowest without-blink saccades (Fig. 10). This is unexpected, because slow peak velocities go along with longer saccade durations. If dynamic overshoots were caused by prolonged OPN inhibition, we would have expected that instead saccades with high peak velocity and short duration would have been the ones most affected. In summary, inhibition of omnipause neurons is a plausible mechanism to explain the time-locking of saccades to blinks, but it is questionable that this alone could cause the occurrence of large dynamic overshoots. The cerebellum plays a crucial role in planning the kinematics of saccades and in blink timing. Given how closely time-locked these two movements are, some form of joint planning appears likely, in particular since dynamic assembly of muscle synergies typically manifest themselves by cerebellar control. A cerebellar contribution to within-blink saccades has so far not been discussed in the literature, but this could be investigated in patients with cerebellar impairment.

It remains unclear to what extent the cocontraction of extraocular muscles might also influence saccade kinematics. Goossens and Van Opstal (13) convincingly demonstrated that cocontraction alone could not account for the changes in saccade kinematics during blinks, but at the same time they could not rule out that cocontraction leads to additional interference with saccade execution on top of that at premotor circuit level. We can think of two ways in which cocontraction could influence saccade kinematics. First, it might be possible that simultaneous activation of oculomotor neurons by the saccade command and the blink-related eye movement command leads to a nonlinear interaction downstream from the saccade premotor circuit. Second, the eyeball retraction might lead to considerable change in pulley position and thus affect the lever arm of the rectus muscles. The neural innervation of rectus muscles for a regularly programmed saccade could then result in an overextended orientation of the eyeball while it is retracted during a blink. Unfortunately, there have not been data quantifying both the amount of

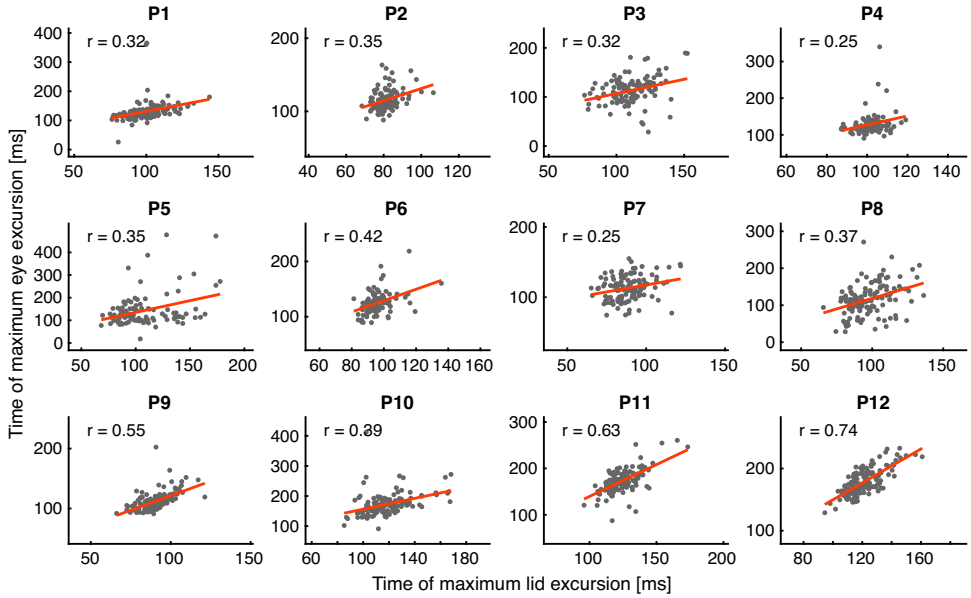

Figure 13. Correlation of blink and saccade metrics. Time of maximum lid excursion relative to blink onset plotted against time of maximum eye excursion during within-blink saccades for all participants. We performed a linear regression analysis on the data and indicate *P* value, Pearson's *r*, and slope in each panel. *P1–P12, participants P1* through *P12*.

cocontraction (or the eyeball retraction it causes) and saccade kinematics. Scleral search coils and EOG measure the rotational component of the BREM but not the eyeball translation, which is arguably the main component of the movement. Dynamic MRI data with its simultaneous measurements of gaze trajectory and eyeball retraction could shed light on this issue. Indeed, the MRI data we obtained from two participants seemed to support the hypothesis that dynamic overshoots are directly linked to eyeball retraction. For a conclusive analysis, however, it will be necessary to measure within-blink saccades of various amplitudes and in both directions from multiple participants. Such a large data set could then unravel which of the various parameters like relative saccade timing, saccade amplitude, blink duration, or eyeball retraction causes the saccade to overshoot. It would be particularly interesting to test whether there is a correlation between some metrics of eyeball retraction and saccade kinematics. If inhibition of the OPNs should account for the dynamic overshoot of within-blink saccades, there should only be a relationship with the duration of eyeball retraction. If otherwise a link between dynamic overshoots and retraction metrics like amplitude, velocity, or return timing would be found, the dynamic overshoots could be at least in part attributed to muscular cocontraction.

Even though EOG does not offer the same precision as scleral search coils, its noninvasive nature made it easy to measure a larger number of participants, which seems especially important considering the individual effects we observed. It should be noted, however, that the presented method is limited to the study of saccadic gaze shifts within blinks. If additional analysis of the blink-related eye movement itself should be required, one would have to use scleral search coils for this. Key results of search coil studies were reproduced, and EOG also offers the simultaneous recording of lid movement to detect and quantify blink metrics. The results of this study indicate that eye movements during blinks cannot simply be described as a superposition of the typical blink-related eye movement and slow but straight saccades. In particular, the presence of large dynamic overshoots seems to support the hypothesis that there is additional mechanical interference due to cocontraction of extraocular muscles. Future studies could investigate the dependence of these dynamic overshoots on varying saccade amplitudes and different saccade directions. The finding of dynamic overshoots adds to the potential of blink-related interference to probe and understand the generation of saccadic eye movements.

DATA AVAILABILITY

All data are available from the corresponding author upon reasonable request.

SUPPLEMENTAL DATA

Supplemental Movie S1: https://doi.org/10.6084/m9.figshare.19525441

Supplemental Movie S2: https://doi.org/10.6084/m9.figshare.19525450

ACKNOWLEDGMENTS

We thank Jochen Bauer for help and expertise in acquiring dynamic MRI data.

GRANTS

This work has received funding from the European Union's Horizon 2020 research and innovation program under Marie Skodowska-Curie Grant Agreement No. 734227.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.K., T.W., N.A.B., and M.L. conceived and designed research; J. K. performed experiments; J.K. analyzed data; J.K., T.W., and M.L. interpreted results of experiments; J.K. prepared figures; J.K. drafted

manuscript; J.K., T.W., N.A.B., and M.L. edited and revised manuscript; J.K., T.W., N.A.B., and M.L. approved final version of manuscript.

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