

# Smooth pursuit inhibition reveals audiovisual enhancement of fast movement control

**Philipp Kreyenmeier**

Department of Ophthalmology & Visual Sciences,  
University of British Columbia, Vancouver,  
British Columbia, Canada  
Graduate Program in Neuroscience,  
University of British Columbia, Vancouver,  
British Columbia, Canada



**Ishmam Bhuiyan**

Department of Ophthalmology & Visual Sciences,  
University of British Columbia, Vancouver,  
British Columbia, Canada



**Mathew Gian**

Department of Ophthalmology & Visual Sciences,  
University of British Columbia, Vancouver,  
British Columbia, Canada



**Hui Mei Chow\***

Department of Ophthalmology & Visual Sciences,  
University of British Columbia, Vancouver,  
British Columbia, Canada  
Department of Psychology, St. Thomas University,  
Fredericton, New Brunswick, Canada



**Miriam Spring\***

Department of Ophthalmology & Visual Sciences,  
University of British Columbia, Vancouver,  
British Columbia, Canada  
Graduate Program in Neuroscience,  
University of British Columbia, Vancouver,  
British Columbia, Canada  
Djavad Mowafaghian Center for Brain Health,  
University of British Columbia, BC, Vancouver, Canada  
Institute for Computing, Information, and Cognitive  
Systems, University of British Columbia,  
Vancouver, BC, Canada



The sudden onset of a visual object or event elicits an inhibition of eye movements at latencies approaching the minimum delay of visuomotor conductance in the brain. Typically, information presented via multiple sensory modalities, such as sound and vision, evokes stronger and more robust responses than unisensory information. Whether and how multisensory information affects ultra-short latency oculomotor inhibition is unknown. In two experiments, we investigate smooth pursuit and saccadic inhibition in

response to multisensory distractors. Observers tracked a horizontally moving dot and were interrupted by an unpredictable visual, auditory, or audiovisual distractor. Distractors elicited a transient inhibition of pursuit eye velocity and catch-up saccade rate within ~100 ms of their onset. Audiovisual distractors evoked stronger oculomotor inhibition than visual- or auditory-only distractors, indicating multisensory response enhancement. Multisensory response enhancement magnitudes were equal to the linear sum of responses

Citation: Kreyenmeier, P., Bhuiyan, I., Gian, M., Chow, H. M., & Spring, M. (2024). Smooth pursuit inhibition reveals audiovisual enhancement of fast movement control. *Journal of Vision*, 24(4):3, 1–17, <https://doi.org/10.1167/jov.24.4.3>.

<https://doi.org/10.1167/jov.24.4.3>

Received September 15, 2023; published April 1, 2024

ISSN 1534-7362 Copyright 2024 The Authors



**to component stimuli. These results demonstrate that multisensory information affects eye movements even at ultra-short latencies, establishing a lower time boundary for multisensory-guided behavior. We conclude that oculomotor circuits must have privileged access to sensory information from multiple modalities, presumably via a fast, subcortical pathway.**

## Introduction

Humans have the remarkable, native ability to react rapidly to novel visual objects or events in their environment. Express saccades can have latencies as short as 80 ms (Fischer & Weber, 1993) and ocular following responses (Miles, Kawano, & Optican, 1986)—a smooth tracking movement in response to sudden-onset large-field visual motion—can be initiated within 85 ms of motion onset (Gellman, Carl, & Miles, 1990). Moreover, the onset of a salient stimulus elicits an involuntary inhibition of microsaccades at ultra-short latencies, a phenomenon known as *oculomotor freezing* (Engbert & Kliegl, 2003; Rolfs, Kliegl, & Engbert, 2008; Hafed & Ignashchenkova, 2013; White & Rolfs, 2016; Abeles, Amit, Tal-Perry, Carrasco, & Yuval-Greenberg, 2020; Buonocore & Hafed, 2023). Such oculomotor inhibition is not limited to saccadic eye movements but has also been observed during smooth pursuit eye movements (Buonocore, Skinner, & Hafed, 2019; Ziv & Bonneh, 2021)—the eyes' key response to moving objects. In response to a task-irrelevant distractor, ongoing pursuit transiently slows down at a latency of  $\sim 110$  ms in humans (Kerzel, Born, & Souto, 2010) and  $\sim 50$  ms in monkeys (Buonocore et al., 2019). These studies demonstrate that oculomotor control circuits must have privileged access to sensory signals, allowing the integration of novel environmental events at ultra-short latencies.

Whereas oculomotor inhibition has often been observed in response to visual stimuli, novel events or objects in our natural environment typically contain both light and sound. In general, such cross-modal stimuli trigger faster and more robust neuronal and behavioral responses than stimuli presented via a single sense, a phenomenon known as multisensory response enhancement (e.g., Meredith & Stein, 1983; Rowland, Quessy, Stanford, & Stein, 2007; Stein & Stanford, 2008). For instance, pupillary responses are stronger when evoked by audiovisual stimuli as compared to unimodal (visual or auditory) targets (Rigato, Rieger, & Romei, 2016; Wang, Blohm, Huang, Boehnke, & Munoz, 2017; Van der Stoep, Van der Smagt, Notaro, Spock, & Naber, 2021). Similarly, saccade latencies (Frens, Van Opstal, & Van der Willigen, 1995; Corneil, Van Wanrooij, Munoz, & Van Opstal, 2002;

Bell, Meredith, Van Opstal, & Munoz, 2005; Wang et al., 2017) and manual reaction times are shorter when observers respond to audiovisual targets (e.g., Van der Stoep et al., 2021, Diederich & Colonius, 2004).

Response amplification in the presence of cross-modal stimuli is likely mediated by a number of different brain areas, including the superior colliculus (SC), a midbrain structure that is critically involved in orienting behavior (Allen, Lawlor, Salles, & Moss, 2021) including eye movements (Corneil & Munoz, 2014). Intermediate and deep SC layers contain neurons that respond to signals from multiple sensory modalities and exhibit increased firing rates in response to cross-modal signals (Meredith & Stein, 1983; Stein & Stanford, 2008). The nature of increased multisensory firing rates can be additive (i.e., multisensory firing rate is equal to the linear sum of the unisensory evoked firing rates), superadditive (i.e., higher firing rate than the linear sum), or sub-additive (i.e., lower firing rate than the linear sum; Stanford, Quessy, & Stein, 2005; Stanford & Stein, 2007; Stevenson et al., 2014). Many aspects of primate behavior show additive or superadditive multisensory response enhancement.

Here we investigate whether and how cross-modal stimuli affect ultrafast oculomotor inhibition. This is an open question, because (micro)saccadic or pursuit inhibition already occurs at latencies that are at the limit of visuomotor conductance in the brain. Whereas microsaccadic inhibition can exhibit multisensory response enhancement (Wang et al., 2017), it is generally difficult to assess additivity or superadditivity in oculomotor inhibition caused by flooring effects. Microsaccade rate, for example, often drops close to zero even in response to unimodal distractors (Rolfs et al., 2008; Wang et al., 2017). One way to overcome this constraint is to investigate pupil responses. However, whereas some studies showed superadditive multisensory pupil responses (Rigato et al., 2016), others observed additive effects (Wang et al., 2017; Van der Stoep et al., 2021). In this study, we use pursuit inhibition to investigate multisensory processing. Pursuit eye movements have two key advantages: (1) In contrast to saccades, which are discrete events, pursuit provides a continuous and gradual response to novel sensory inputs, and (2) Compared to pupil orienting, pursuit inhibition occurs more quickly, providing a fine-tuned window into the temporal evolution of ultrafast sensorimotor responses. Whereas previous studies have established pursuit inhibition in response to unimodal distractors (Kerzel et al., 2010), here we combine signals across both senses to investigate the nature and time course of multisensory inhibition and compare effects on pursuit and catch-up saccades.

## Methods

We conducted two experiments. The study design, sample size, and analyses of the main experiment were preregistered on the Open Science Framework (<https://osf.io/yc3w6>). A control experiment was conducted to rule out potential confounds and replicate the main findings at low stimulus contrast. The following study methods apply to the main, preregistered experiment. Differences between the main and control experiment are described below.

### Observers

We present data from 16 human observers (nine female;  $26.6 \pm 5.6$  years; mean  $\pm$  SD; four authors) with normal or corrected-to-normal visual acuity and no history of neurological, psychiatric, or eye disease. The sample size was determined using an a priori power analysis (G\*Power; [Faul, Erdfelder, Lang, & Buchner, 2007](#)) with  $\alpha = 0.05$  and power = 0.80. Our estimated effect size of  $d = 0.67$  was based on pilot data (not included) obtained in  $n = 10$  observers. Data from one additional observer were excluded from data analysis because they failed to reliably track the moving target (resulting in  $>50\%$  excluded trials). The experimental procedure was in accordance with the Declaration of Helsinki and approved by the University of British Columbia Behavioral Research Ethics Board. All observers gave written informed consent and were remunerated at a rate of \$10/hour for their participation.

### Apparatus

Observers performed the experiment in a dimly lit laboratory. Stimuli were presented on a gamma-corrected 40.6 cm  $\times$  29.8 cm CRT monitor (ViewSonic G255; 85 Hz; 1600  $\times$  1200 pixels; ViewSonic, Brea, CA, USA) positioned at a viewing distance of 50 cm. An Eyelink 1000 Tower Mount (SR Research, Kanata, ON, Canada) video-based eye tracker recorded observers' right eye position at a sampling rate of 1 kHz. Observers' head and chin were supported by a combined forehead and chin rest to minimize head movements. Stimulus presentation and data collection procedures were programmed in MATLAB R2019a (The MathWorks Inc., Natick, MA, USA) using the Eyelink and Psychophysics (version 3.0.12; [Cornelissen, Peters, & Palmer, 2002](#); [Kleiner et al., 2007](#)) toolboxes. Auditory distractors were presented through speakers (EP-691H; SpecResearch, Walnut, CA, USA) placed on either side of the screen (45 cm apart), at a distance of 89 cm from observers.

### Stimuli and procedure

The pursuit target was a small, white Gaussian dot with a standard deviation of  $0.14^\circ$ , presented on a gray background. At the start of each trial, the target was presented  $10^\circ$  to the left of the screen center and then followed a step-ramp motion sequence ([Figure 1A](#)): After successful fixation, the target stepped  $2^\circ$  further to the left and then moved rightward across the screen at a constant velocity of  $10^\circ/s$  for 2000 ms. Observers were instructed to track the target closely with their eyes until it disappeared from view, marking the end of the trial. In 60% of the trials, a distractor was presented at an unpredictable time within a time window of 500–1500 ms after ramp onset. Of all distractor trials, 1/3 contained a visual distractor, 1/3 an auditory distractor, and 1/3 a combined audiovisual distractor. The visual distractor was presented for 50 ms and consisted of two horizontally-oriented, sinusoidal gratings (1.5 cycles; spatial frequency = 1 cycle per degree; contrast level = 100%), spanning the entire screen width and located  $5^\circ$  above and below the target's horizontal trajectory. Because the visual distractor consisted of a horizontally oriented sinusoidal grating, it does not cause retinal motion in the opposite direction of smooth pursuit. A high-contrast, low spatial frequency grating was chosen based on previous studies showing that fast orienting responses are preferentially evoked by high contrast and low spatial frequency stimuli ([Kozak, Kreyenmeier, Gu, Johnston, & Corneil, 2019](#); [Ziv & Bonneh, 2021](#)). The auditory distractor consisted of a 60 dBA white noise sound, presented for 50 ms via both speakers (measured background noise in the laboratory:  $\sim 41$  dBA). In the audiovisual distractor condition, both distractors were presented simultaneously. In the remaining 40% of trials, no distractor was presented (control condition).

The experiment was split into 10 blocks of 50 trials each (500 trials in total; 100 in each of the three experimental conditions and 200 in the control condition). Trials were presented in a pseudorandom order. The experiment took approximately 60 minutes to complete.

### Data analyses

#### *Eye movement data preprocessing*

To investigate the impact of unisensory versus multisensory distractors on rapid oculomotor inhibition, we analyzed pursuit in a time window from 200 ms before to 400 ms after distractor onset. First, we time-locked all eye movement position traces to the onset of the distractor. For the control condition, we sampled eye movement traces from the

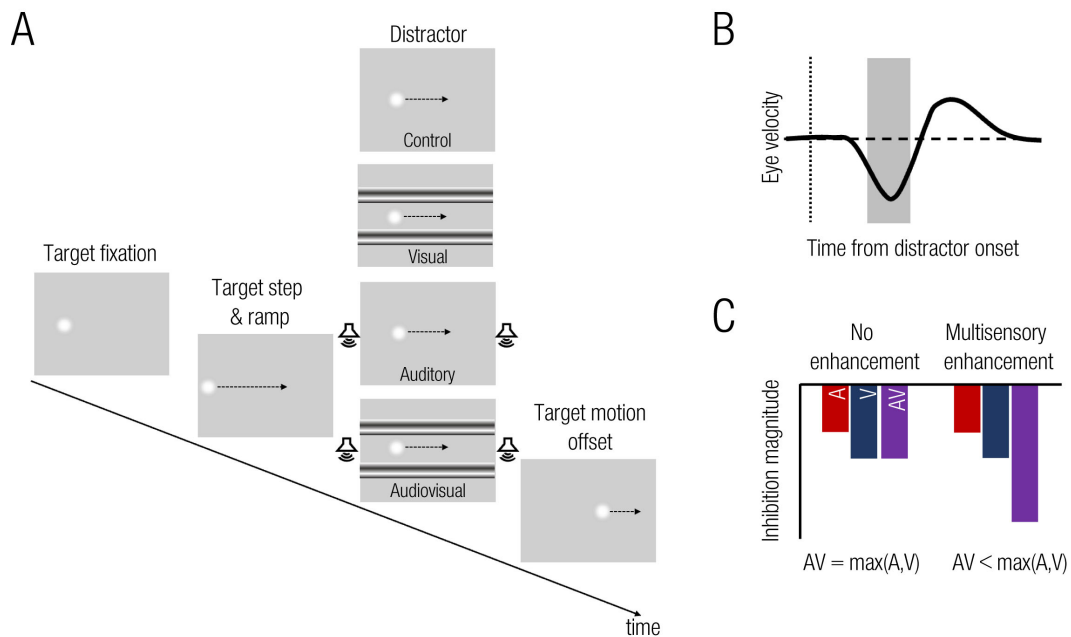


Figure 1. (A) Experimental paradigm. Observers tracked a white Gaussian target moving horizontally from left to right. At an unpredictable time (500 to 1500 ms after target onset), a visual (striped pattern), an auditory (white noise), or audiovisual distractor was presented for 30 ms. In the control condition, no distractor was presented. Observers were instructed to track the target until it disappeared, marking the end of the trial. (B) Expected inhibition response in pursuit eye velocity evoked by distractor onset (dotted vertical line). An initial, transient inhibition (highlighted grey area) is followed by a rebound period. (C) Visualization of the main hypothesis. A, auditory; AV, audiovisual; V, visual.

same distribution as in the experimental conditions to ensure that eye movement traces from all conditions were sampled over similar time windows. Next, we derived eye velocity traces by digital differentiation of the continuous eye position data. Velocity traces were then filtered using a second-order Butterworth filter with a cut-off frequency of 40 Hz. We detected catch-up saccades using a velocity threshold (30°/s), which had to be exceeded for at least five successive frames. The emphasis of our analysis is on the smooth component of the pursuit eye movement, particularly, on pursuit velocity. However, catch-up saccades form an integral part of the pursuit response (Orban de Xivry & Lefèvre, 2007; Goettker & Gegenfurtner, 2021), and we therefore also analyzed the rate of catch-up saccades over time for each observer and experimental condition. Catch-up saccade rates were calculated by summing saccade onsets per observer and condition at each time point. We then calculated a moving average applying a causal smoothing kernel  $\omega(\tau) = \alpha^2 \tau \exp(-\alpha\tau)$  with a temporal decay parameter of  $\alpha = \frac{1}{25} \text{ms}$  (for details, see Rolfs et al., 2008; Widmann, Engbert, & Schröger, 2014; White & Rolfs, 2016). Time-varying saccade rates were then normalized by the number of trials and multiplied by the sampling rate to convert into units per second (Hz). All trials were manually inspected and trials with blinks, undetected saccades, and trials where the eye tracker lost the

signal were excluded from further analyses (1.3% of trials).

### Analysis of smooth pursuit and saccade inhibition

Based on previous studies (Kerzel et al., 2010; Buonocore et al., 2019; Ziv & Bonneh, 2021) we expected the sudden onset of a visual or auditory distractor to elicit a short-latency, transient inhibition of smooth pursuit eye velocity, followed by a rebound period during which pursuit velocity rises above the baseline (Figure 1B). The focus of our analyses is on the latency and magnitude of the early pursuit inhibition response as a measure of multisensory response enhancement. To determine the inhibition onset latency for each experimental condition, we used the jackknife procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). This method allows accurate detection of small modulations in noisy data. It has been applied to the analysis of event-related potentials (Luck, 2014), modulations in continuous eye movements, such as pupil responses (Grenzbach, Wegner, Einhäuser, & Bendixen, 2021) or smooth pursuit eye movements (Kerzel et al., 2010). In short, for each condition and observer, we first computed leave-one-out ( $n - 1$ ) grand averages. From each grand average, we then determined the maximum dip in eye velocity during the inhibition time window (0 to 200 ms

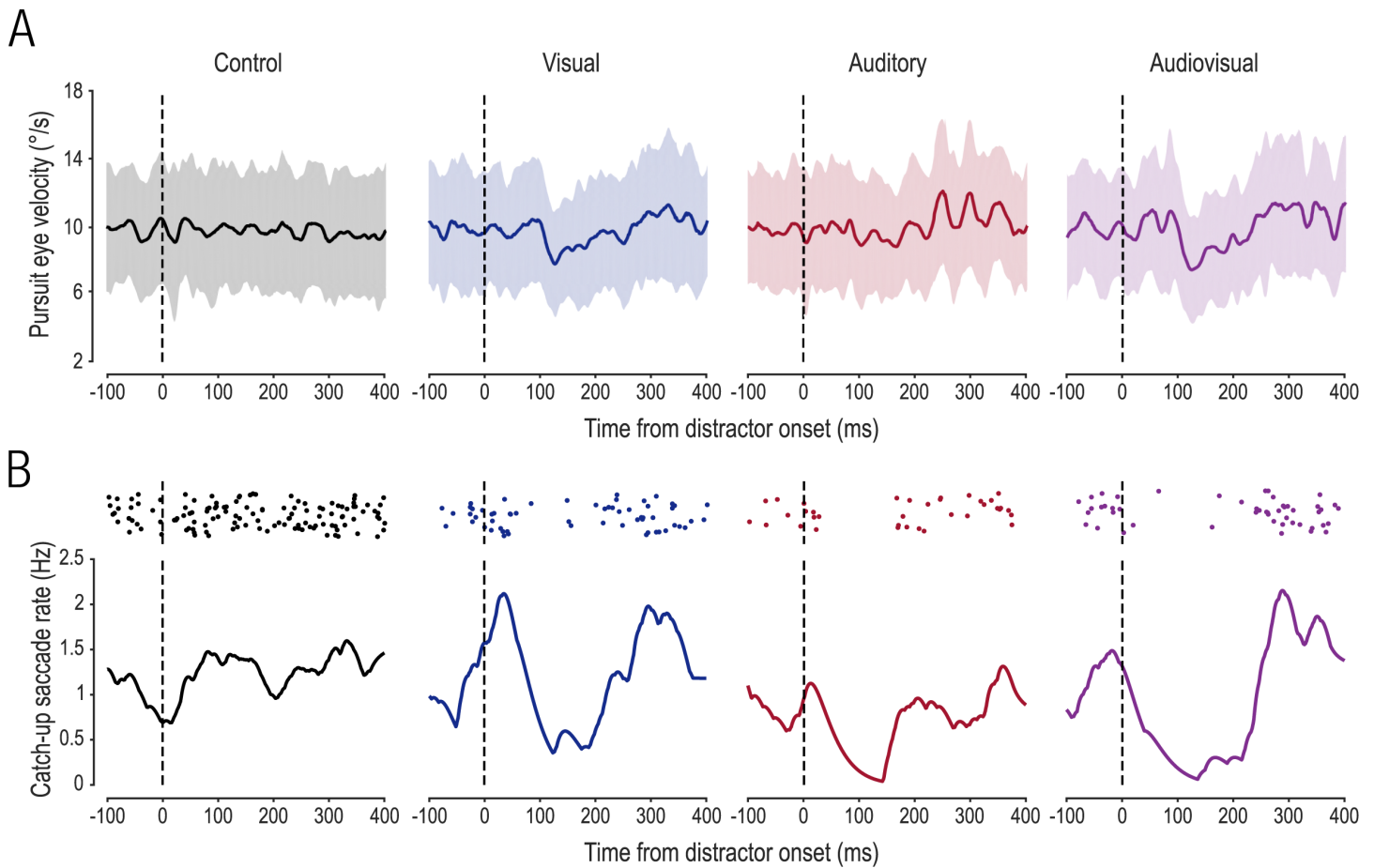


Figure 2. Pursuit velocity and catch-up saccade rates from one representative observer. (A) Mean horizontal smooth pursuit velocity across trials (bold traces). Shaded area shows  $\pm 1$  SD. (B) Raster plots of catch-up saccade onsets (upper panels) and normalized catch-up saccade rates over time (lower panels) across all trials for this observer. Higher overall number of catch-up saccades (upper panel in B) in the control condition was due to the higher trial number in this condition. All data are aligned to distractor onset (dashed lines).

after distractor onset) and defined the inhibition onset latency as the first time point at which eye velocity fell below 50% of the peak inhibition. To account for the reduced variability when basing an analysis on grand averages, we used corrected  $F$ -values ( $F_{corr} = F/[n - 1]^2$ ) when statistically comparing latencies between experimental conditions (Luck, 2014). The magnitude of the inhibition response was then defined as the pursuit velocity over a 50-ms time window starting at the mean inhibition onset latency for each observer and condition. Within each experimental condition, we compared the inhibition magnitude to mean baseline pursuit, calculated over a time window from  $-100$  to  $0$  ms before distractor onset. We applied the same jackknife method to detect inhibition onsets for saccade rates as used for pursuit. Similar to pursuit inhibition magnitude, saccade inhibition magnitude was determined over a 50-ms time window starting at the time point at which mean saccade rate fell below 90% of peak inhibition. A higher relative criterion was used

to account for the wider shape of saccade inhibition compared to pursuit inhibition (compare Figure 2 and Figure 3).

## Hypotheses and statistical analyses

We analyzed the data in three parts: (1) We confirmed that visual, auditory, and audiovisual distractors elicited a detectable pursuit inhibition response. We compared pursuit baseline and inhibition magnitude using three separate  $t$ -tests, one for each experimental condition, with a corrected alpha level of 0.0167. (2) To test whether pursuit inhibition showed a significant multisensory enhancement (Figure 1C), we compared pursuit inhibition magnitudes between the three distractor conditions using a one-way repeated-measures analysis of variance (rmANOVA) with factor *distractor type*. All post hoc comparisons were Bonferroni corrected (Abdi, 2007) to test the

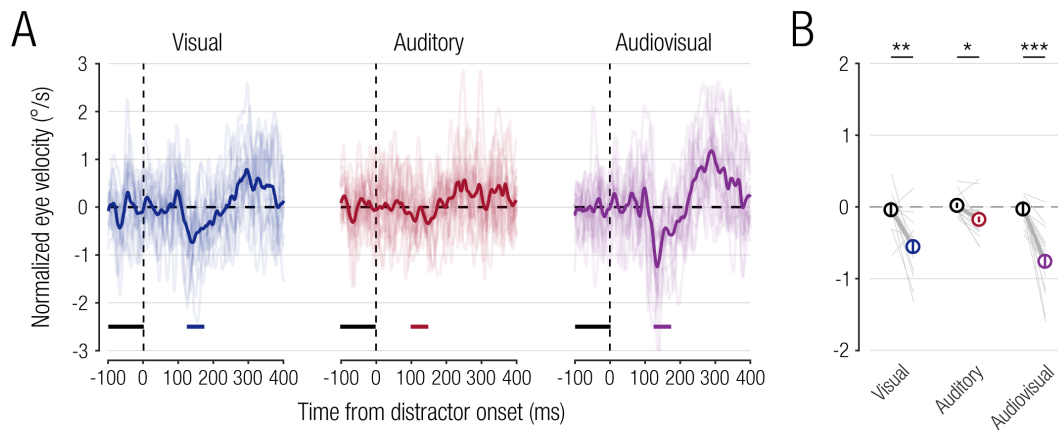


Figure 3. (A) Normalized mean pursuit velocity for individual observers (thin lines) and across observers (bold lines). All data were aligned to distractor onset. Horizontal line segments at the bottom of each panel indicate analysis time windows used to calculate baseline pursuit (black) and inhibition magnitudes (colored). (B) Comparison of baseline pursuit and inhibition magnitudes for different distractor types. Circles and error bars denote mean  $\pm 1$  within-subject SEM. Thin gray lines show individual observer data. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

collective proposition that the audiovisual distractor elicited significantly stronger inhibition magnitudes across pursuit and saccade measures as compared to the unisensory (visual or auditory) distractors. For all  $t$ -tests, we report the Bayes factor ( $BF_{10}$ ), allowing us to assess evidence for the absence of an effect (Keysers, Gazzola, & Wagenmakers, 2020). Following established guidelines, we interpret a  $BF_{10}$  of  $>3$  and  $>10$  as moderate and strong evidence for the presence of an effect and a  $BF_{10}$  of  $<1/3$  and  $<1/10$  as moderate and strong evidence for the absence of an effect (Jeffreys, 1961). (3) Multisensory response enhancement is often described as the result of an additive or a superadditive combination of unisensory conditions (Stevenson et al., 2014). We tested these two alternative hypotheses using a linear mixed-effects model on the inhibition magnitudes. We modeled our data as a function of auditory and visual distractor presence or absence, resulting in a 2 (auditory distractor present versus absent)  $\times$  2 (visual distractor present versus absent) design. If the audiovisual inhibition magnitude can be explained by the linear sum of the unisensory conditions, we would expect significant main effects of visual and auditory distractors but no significant interaction term. Conversely, if the audiovisual condition produced stronger inhibition than the linear sum of the unisensory conditions, we would additionally expect a significant interaction term. We built the following full model that included both main and interaction effects:

$$\text{Inhibition Magnitude} \sim \text{Visual Distractor} \\ * \text{Auditory Distractor} + (1 \mid \text{observer}).$$

We then compared this full model to a reduced model that only contained the two main effects:

$$\text{Inhibition Magnitude} \sim \text{Visual Distractor} \\ + \text{Auditory Distractor} + (1 \mid \text{observer}).$$

All statistical analyses were performed in R (R Core Team, 2022) with an alpha level of .05 (unless otherwise stated).

#### **Divergence from the preregistered analysis plan**

According to our initial analysis plan, we aimed to first assess whether the distractors evoked a short-latency inhibition response during smooth pursuit eye movements by comparing inhibition magnitudes between experimental conditions and the control condition using a one-way rmANOVA. We diverged from this plan to account for unequal trial numbers in the control (200 trials per observer) and experimental conditions (100 trials per observer per condition). Additionally, the well-known phenomenon of anticipatory slowing in pursuit velocity toward the end of a trial is problematic in a design that randomizes the onset time of a distractor. To account for this, we first normalized each observers' pursuit velocity data and then compared inhibition magnitude to a mean baseline pursuit velocity before the distractor onset within each experimental condition (see Kerzel et al., 2010). The originally planned analysis yielded similar results.

## Control experiment

We recruited an additional 16 observers (eight female;  $24.7 \pm 3.8$  years; mean  $\pm$  SD; ten observers not tested in the main experiment). Study methods were the same between the main and control experiment with the following exceptions: (1) Visual stimuli were presented on a ViewSonic G90fB CRT monitor (85Hz;  $1280 \times 1040$  pixels), (2) Visual distractors were presented at three different contrast levels (6.25%, 25%, and 50%), resulting in eight experimental conditions: three visual distractor conditions (each at a different contrast), three audiovisual distractor conditions, one control condition (no distractor), and one auditory distractor condition, presented in pseudorandom order and each repeated 60 times.

## Results

Observers used a combination of smooth pursuit eye movements and catch-up saccades to track the moving target. [Figure 2](#) shows data from one representative observer, who had a mean pursuit velocity of approximately  $10^\circ/\text{s}$  ([Figure 2A](#); left panel), closely matching target velocity, and a catch-up saccade rate of  $\sim 1.2$  Hz ([Figure 2B](#); left panel). In this observer, distractors elicited a transient reduction in pursuit velocity and saccade rate  $\sim 100$  ms after distractor onset ([Figure 2](#)).

### Distractors elicit transient pursuit and catch-up saccade inhibition

Patterns of inhibitory pursuit responses described for the single observer were similar across all observers ([Figure 3A](#)). During the analysis time window ( $-200$

to 400 ms from distractor onset), observers tracked the target with a high mean velocity gain of 1.06 and made an average of 0.7 catch-up saccades per trial. We first confirmed whether different distractors elicited detectable pursuit inhibition responses. To account for individual differences and anticipatory slowing in pursuit, we first normalized pursuit velocity by subtracting the control condition. We then compared mean pursuit velocity during a 50-ms time window from inhibition onset to baseline pursuit in a 100-ms time window before distractor onset. We found a significant reduction in normalized pursuit velocity as compared to baseline pursuit for all three distractor types. The visual distractor elicited a mean velocity reduction of  $\sim 0.52^\circ/\text{s}$  (equivalent to a 5.2% reduction in pursuit velocity gain;  $t(15) = -4.23$ ;  $p = 0.002$ ;  $d = 1.06$ ;  $BF_{10} = 50.48$ ). The auditory distractor resulted in a small, yet significant reduction in pursuit velocity of  $\sim 0.20^\circ/\text{s}$  ( $t(15) = -3.48$ ;  $p = 0.010$ ;  $d = .87$ ;  $BF_{10} = 13.59$ ). The strongest reduction was observed for the audiovisual distractor, with a mean reduction of  $\sim 0.73^\circ/\text{s}$  ( $t(15) = -6.53$ ;  $p < 0.001$ ;  $d = 1.63$ ;  $BF_{10} > 1000$ ; [Figure 3B](#)). Thus all three distractors elicited significant inhibition in pursuit velocity. Moreover, pursuit inhibition responses occurred at short latencies of 93.4 ms to the auditory distractor, 120.5 ms to the visual, and 123.3 ms to the audiovisual distractor (rmANOVA on inhibition latency revealed no differences between distractor types,  $F_{corr} < 1$ ).

We next analyzed distractor effects on the catch-up saccade rate as an integral part of the pursuit response ([De Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002](#); [Orban de Xivry & Lefèvre, 2007](#); [Goettker & Gegenfurtner, 2021](#)). Distractor-induced modulations of catch-up saccade rate followed a similar pattern and time course as observed for smooth pursuit. Distractors elicited a rapid reduction in saccade rate, followed by a rebound ([Figure 4A](#)). Saccade rate started to drop

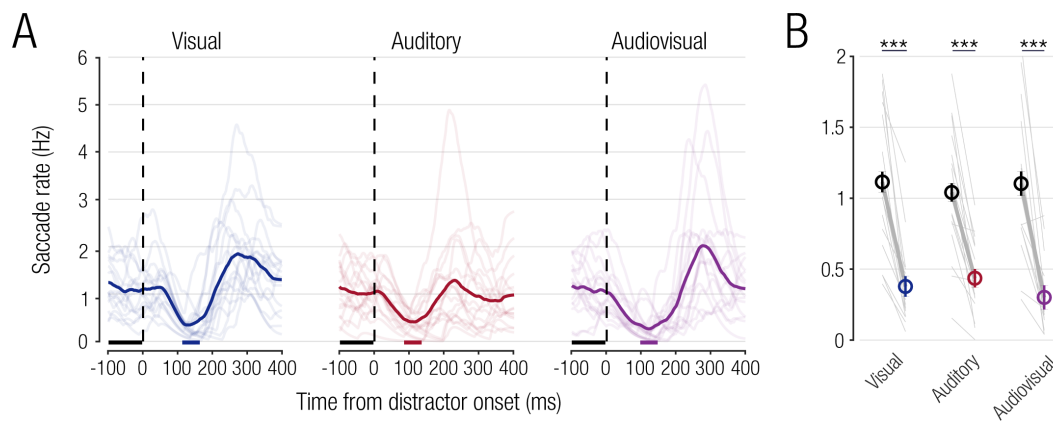


Figure 4. Catch-up saccade rates. (A) Individual (thin lines) and mean catch-up saccade rates across 16 observers (bold lines). (B) Comparison of baseline catch-up saccade rate and inhibition magnitudes for different distractor types. Same conventions as in [Figure 3](#).

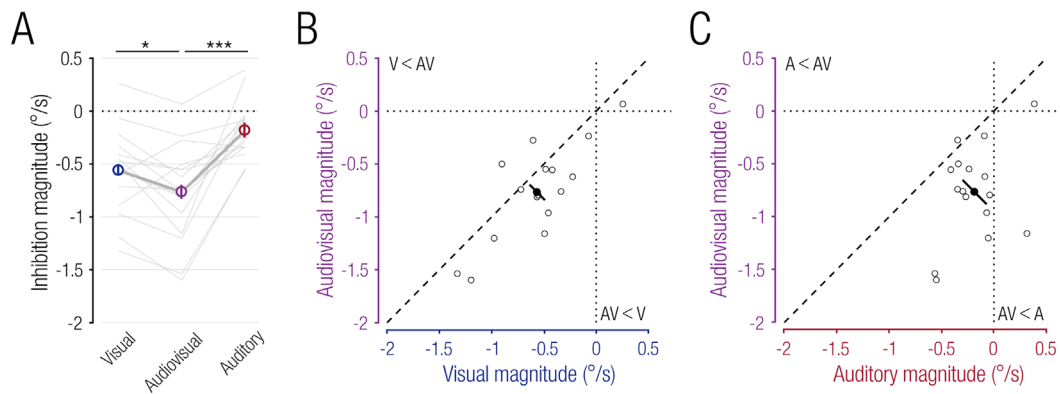


Figure 5. (A) Mean pursuit inhibition magnitudes. Individual observer trends plotted as thin gray lines. Colored discs and error bars represent mean  $\pm 1$  within-subject SEM. (B–C) Comparison of inhibition magnitudes between unimodal and cross-modal conditions for (B) visual and (C) auditory distractors. Open circles are individual observer data, and filled circles represent the mean across observers. Error bars show the 95% confidence interval of the mean difference.

at around 70 ms for the visual distractor and almost immediately after distractor onset for the auditory and audiovisual condition. All three distractors elicited significant reductions in catch-up saccade rates compared to baseline (visual:  $t(15) = -7.18$ ;  $p < 0.001$ ;  $d = 1.80$ ;  $BF_{10} > 1000$ , auditory:  $t(15) = -6.61$ ;  $p < 0.001$ ;  $d = 1.65$ ;  $BF_{10} > 1000$ , and audiovisual:  $t(15) = -6.53$ ;  $p < 0.001$ ;  $d = 1.63$ ;  $BF_{10} > 1000$ ; Figure 4B).

### Multisensory response enhancement in pursuit inhibition

We next compared pursuit inhibition magnitudes across distractor conditions and asked whether the audiovisual distractor elicited stronger inhibition as compared to the visual or auditory distractors. A one-way rmANOVA yielded a significant main effect of *distractor type* on inhibition magnitudes ( $F(1.47, 22.09) = 24.0$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.74$ ; Figure 5A). Pairwise post-hoc comparisons revealed significantly stronger inhibition in the audiovisual condition as compared to visual ( $t(15) = -2.96$ ;  $p = 0.019$ ;  $d = 0.74$ ;  $BF_{10} = 5.64$ ; Figure 5B) and auditory distractors alone ( $t(15) = -5.41$ ;  $p < 0.001$ ;  $d = 1.35$ ;  $BF_{10} = 376.73$ ; Figure 5C). Figures 5B and 5C show individual and mean inhibition responses to visual (Figure 5B) and auditory (Figure 5C) distractors compared to the audiovisual distractor. Data points falling along the diagonal indicate similar inhibition responses for unimodal and audiovisual distractors, whereas data points falling below the diagonal indicate stronger inhibition in the audiovisual condition. These results demonstrate that the audiovisual distractor evokes a significantly stronger inhibition effect compared to the unimodal distractors, indicating multisensory response enhancement.

Similar to pursuit, the audiovisual distractor also evoked the strongest inhibition of catch-up saccades (Figure 4B). Yet, comparing saccade inhibition magnitudes between visual, auditory, and audiovisual distractors did not reveal a significant effect of *distractor type* on saccade inhibition magnitude ( $F(2, 30) = 1.73$ ;  $p = 0.195$ ). This was likely due to a flooring effect: in several observers, and in contrast to what was observed for pursuit, unimodal distractors evoked a decrease in saccade rate to a value close to zero (e.g., Figure 2B) so that no further response enhancement was possible. The following analyses focus on the pursuit component of the inhibition response.

### Additive effect of multisensory integration in pursuit inhibition

Multisensory response enhancement is often attributed to additive or superadditive integration of multisensory signals (Stanford et al., 2005; Stanford & Stein, 2007; Stevenson et al., 2014). We next sought to investigate whether the stronger inhibition response in the audiovisual condition could be explained by an additive or superadditive multisensory effect. To compare these two competing predictions, we analyzed pursuit magnitude as a function of the presence or absence of the visual and auditory distractor. For this analysis, we used mean pursuit velocity from all trials across a 50-ms time window relative to the audiovisual inhibition onset. We ran a linear mixed-effects model with fixed effects *visual distractor* (present versus absent) and *auditory distractor* (present versus absent) and random intercepts per observer.

If the multisensory response enhancement resulted from an additive combination of responses in unimodal conditions, we would observe significant main effects



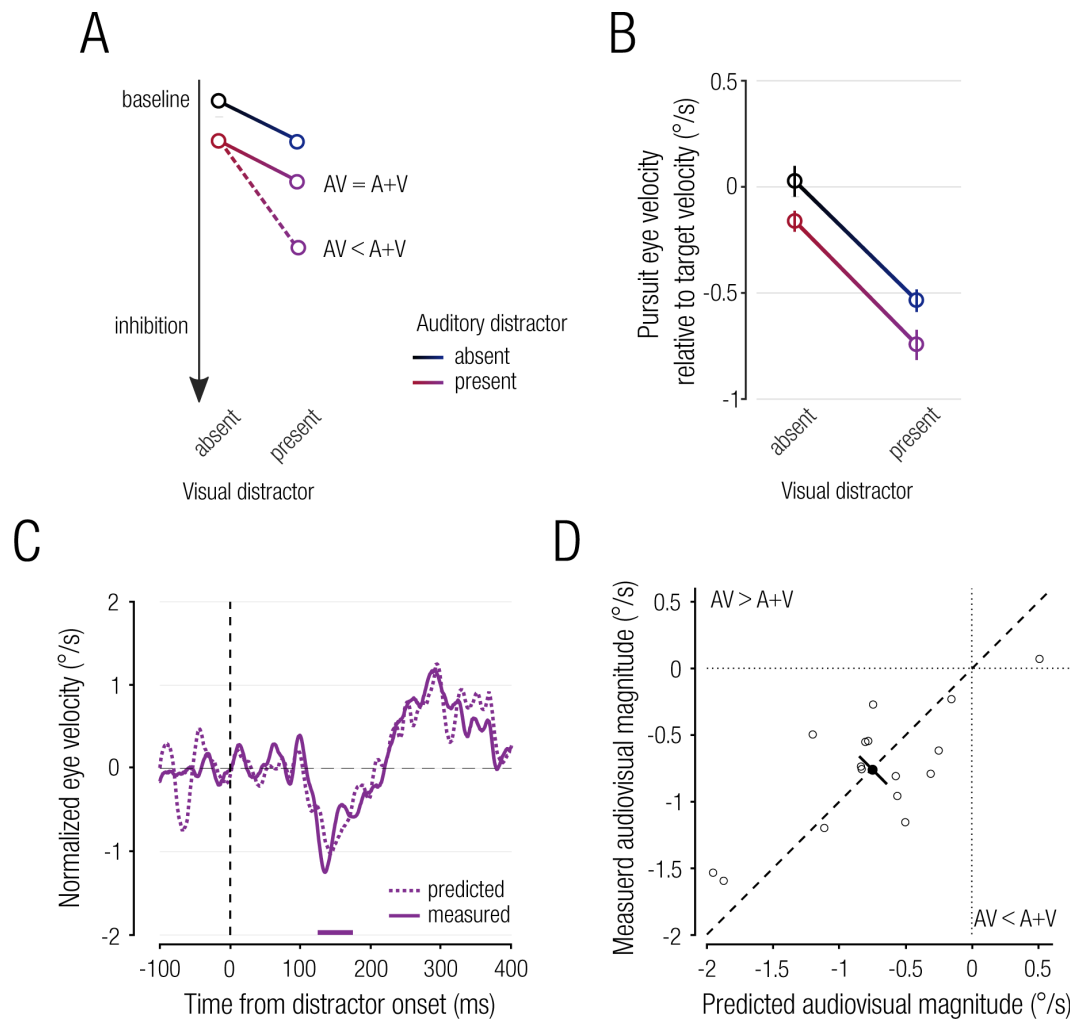


Figure 6. (A) Predictions of additive ( $AV = A + V$ ) and superadditive ( $AV < A + V$ ) effects of multisensory response enhancement on pursuit inhibition. (B) Observed inhibition responses as a function of the presence or absence of the visual and auditory distractors. (C) Mean measured normalized pursuit velocity in the audiovisual condition (solid line) and mean predicted pursuit velocity based on the linear sum of the measured unisensory conditions (dashed line). (D) Comparison of predicted and measured inhibition magnitudes. Open circles are individual observer data and filled circles represent the mean across observers. Error bars show the 95% confidence interval of the mean difference. A, auditory; AV, audiovisual; V, visual.

of both distractor types but no interaction effect (Figure 6A). Following this logic, the multisensory response can be predicted by adding the effects of the visual distractor (baseline versus visual distractor only) and auditory distractor (baseline versus auditory distractor only). Conversely, a superadditive effect would predict a significant interaction term between the two distractor types (i.e., stronger effect if both distractors are present compared to the linear sum of both distractors; Figure 6A). The full model revealed main effects of the visual ( $F(1,7731) = 133.06$ ;  $p < 0.001$ ) and auditory distractors ( $F(1,7731) = 15.56$ ;  $p < 0.001$ ) and no interaction effect ( $F(1,7731) = 0.11$ ;  $p = 0.741$ ; Figure 6B). Comparing the full model to a reduced model without the interaction term did not yield a significant difference between models ( $\chi^2(1) = 0.11$ ;  $p = 0.741$ ; AIC for full model:

33,676 versus reduced model: 33,674), indicating that the observed multisensory response enhancement was not superadditive. To test the alternative that the multisensory response was additive, we used data from the unimodal conditions to predict an additive response. Indeed, a comparison of the predicted (dashed line in Figure 6C) and measured audiovisual responses (solid line in Figure 6C) revealed no significant difference ( $t(15) = 0.18$ ;  $p = 0.860$ ;  $d = 0.04$ ;  $BF_{10} = 0.26$ ; Figure 6D). A Bayes factor  $< 0.33$  indicates moderate evidence in favor of the null hypothesis that there is no difference between the predicted and measured inhibition magnitudes. Therefore the enhanced pursuit inhibition caused by the audiovisual distractor can be well explained by an additive combination of the component stimuli.

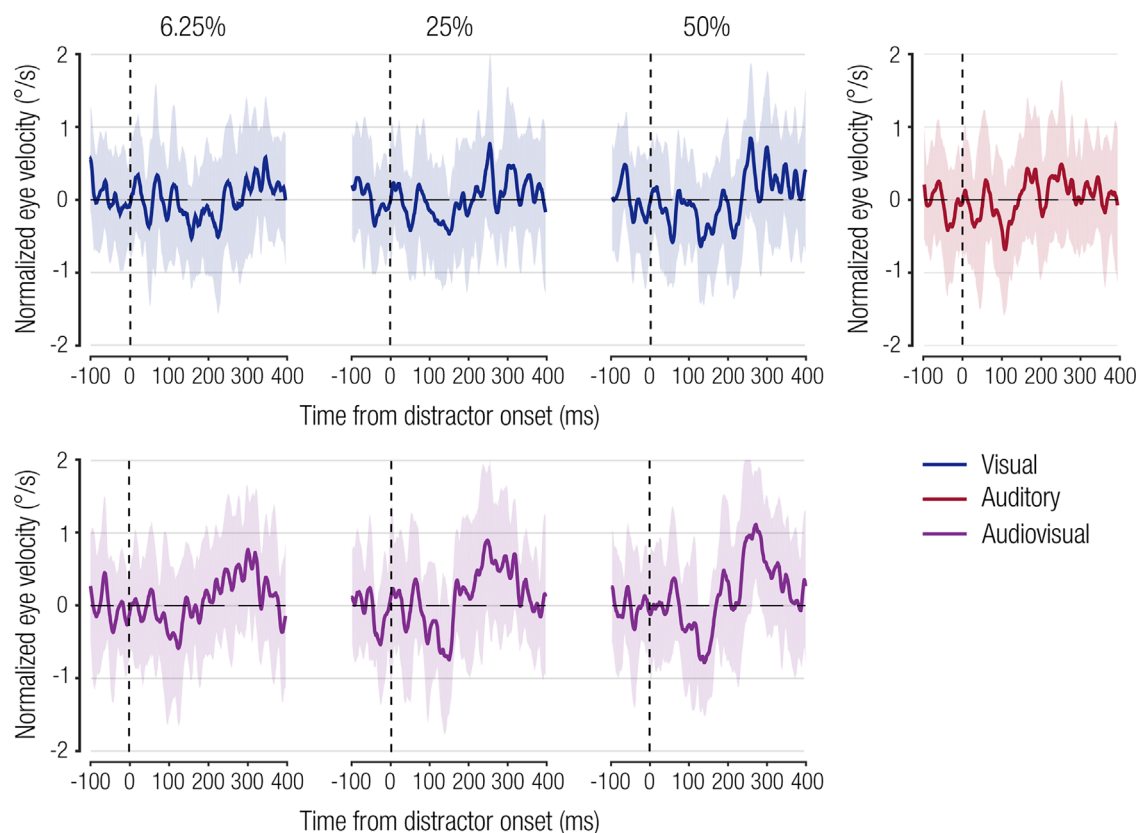


Figure 7. Distractor effect on pursuit eye velocity in the control experiment using different visual contrast levels (6.25%, 25%, and 50%). Bold lines represent means across observers, and shaded areas represent  $\pm 1$  SD.

### Additive signal integration at low distractor contrast

The multisensory response enhancement observed in pursuit inhibition magnitude can be explained by an

additive effect. Similar findings have been obtained with pupil responses to multisensory stimuli (Van der Stoep et al., 2021). Van der Stoep and colleagues’ study and our main experiment used high-contrast visual stimuli, potentially causing a flooring effect in pursuit inhibition

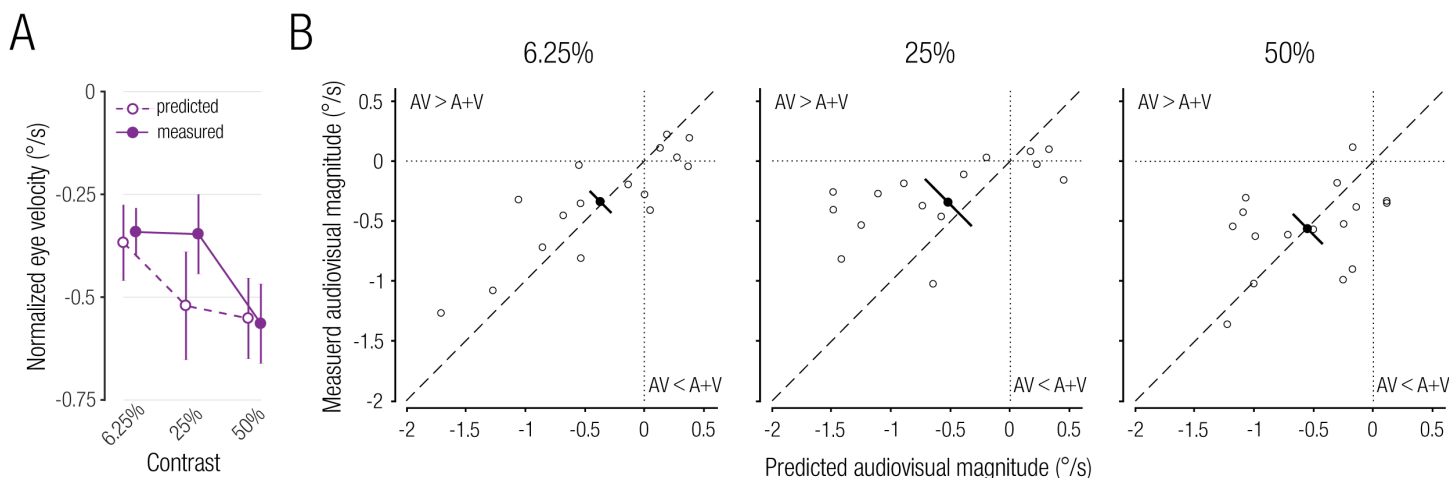


Figure 8. (A) Mean measured (solid lines, filled circles) and predicted (dashed lines, open circles) pursuit inhibition magnitudes in response to the audiovisual distractors. Error bars show  $\pm 1$  within-subject SEM. (B) Comparison of predicted and measured inhibition magnitudes. Open circles show individual data and filled circles represent means across observers. Error bars show 95% CI of the mean difference between conditions. Note, the noisier pursuit velocity traces were due to the lower number of trials per condition in the control experiment.

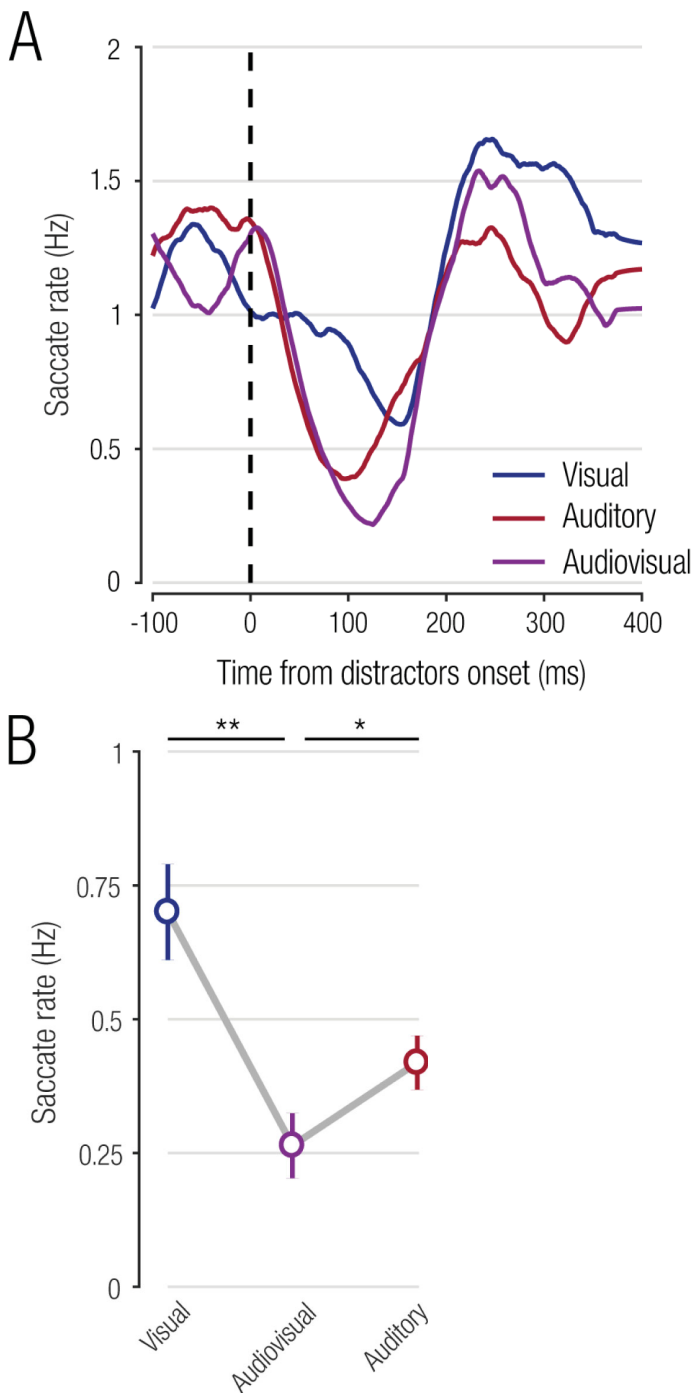


Figure 9. (A) Mean saccade rate from the low-contrast condition (contrast: 6.25%) in Experiment 2. (B) Mean saccade inhibition magnitudes. Error bars show  $\pm 1$  within-subject SEM.

(or pupil responses). Therefore, to assess whether additive effects of multisensory response enhancement hold for low-intensity stimuli, we manipulated visual distractor contrast in a control experiment. Observers performed the same task as in the main experiment, but with the visual distractor presented at either 6.25%, 25%, or 50% contrast.

Figure 7 shows that pursuit eye velocity traces were noisier, likely due to the lower number of trials

per condition. Yet, we observed the same transient distractor-induced inhibition in pursuit eye velocity as in the main experiment. We assessed whether an additive combination of auditory and visual distractors predicted responses evoked by audiovisual distractors, akin to the main experiment. Mean pursuit inhibition magnitudes in the audiovisual condition were well predicted by additive combination of the component stimuli across all visual contrast levels (Figure 8A). Congruently, we found no differences between predicted and observed responses for any of the three contrast levels and Bayes factors imply moderate evidence for the absence of an effect (6.25% contrast:  $t(15) = 0.31$ ;  $p = 1$ ;  $d = 0.08$ ;  $BF_{10} = .27$ ; 25% contrast:  $t(15) = 0.94$ ;  $p = 1$ ;  $d = 0.24$ ;  $BF_{10} = 0.38$ ; 50% contrast:  $t(15) = -0.11$ ;  $p = 1$ ;  $d = 0.03$ ;  $BF_{10} = .26$ ; Figure 8B). These findings indicate that an additive combination of auditory and visual distractors could explain pursuit inhibition to audiovisual distractors, irrespective of contrast levels.

In the main experiment, we did not find multisensory response enhancement in catch-up saccade inhibition, likely because of a flooring effect in saccade rate in response to high-contrast visual distractors (see Figure 4). Our control experiment allowed us to assess whether multisensory response enhancement is observed in catch-up saccade inhibition when probed with low-contrast distractors. Therefore we additionally analyzed catch-up saccade rates of the low-contrast condition (6.25%; Figure 9). We observed stronger saccade inhibition in response to the audiovisual distractor as compared to visual or auditory distractors. These findings indicate that audiovisual distractors enhance catch-up saccade inhibition similar to the pattern we observed for smooth pursuit inhibition (see Figure 5A).

## Discussion

Oculomotor inhibition in response to sudden-onset distractors occurs at ultra-short latencies and provides a behavioral measure of rapid visuomotor processes in the human brain. We used smooth pursuit eye velocity and catch-up saccade rate to probe oculomotor inhibition in response to visual, auditory, or audiovisual distractors. Distractor onsets elicited a rapid decrease in pursuit eye velocity and catch-up saccade rate. Critically, when probed with synchronous audiovisual distractors, pursuit inhibition was significantly stronger as compared to either visual or auditory distractors alone, indicating multisensory response enhancement. An oculomotor orienting response that is enhanced by cross-modal stimulation might be an advantageous mechanism to increase an organism's efficiency in detecting and discriminating between sudden external events in the environment.

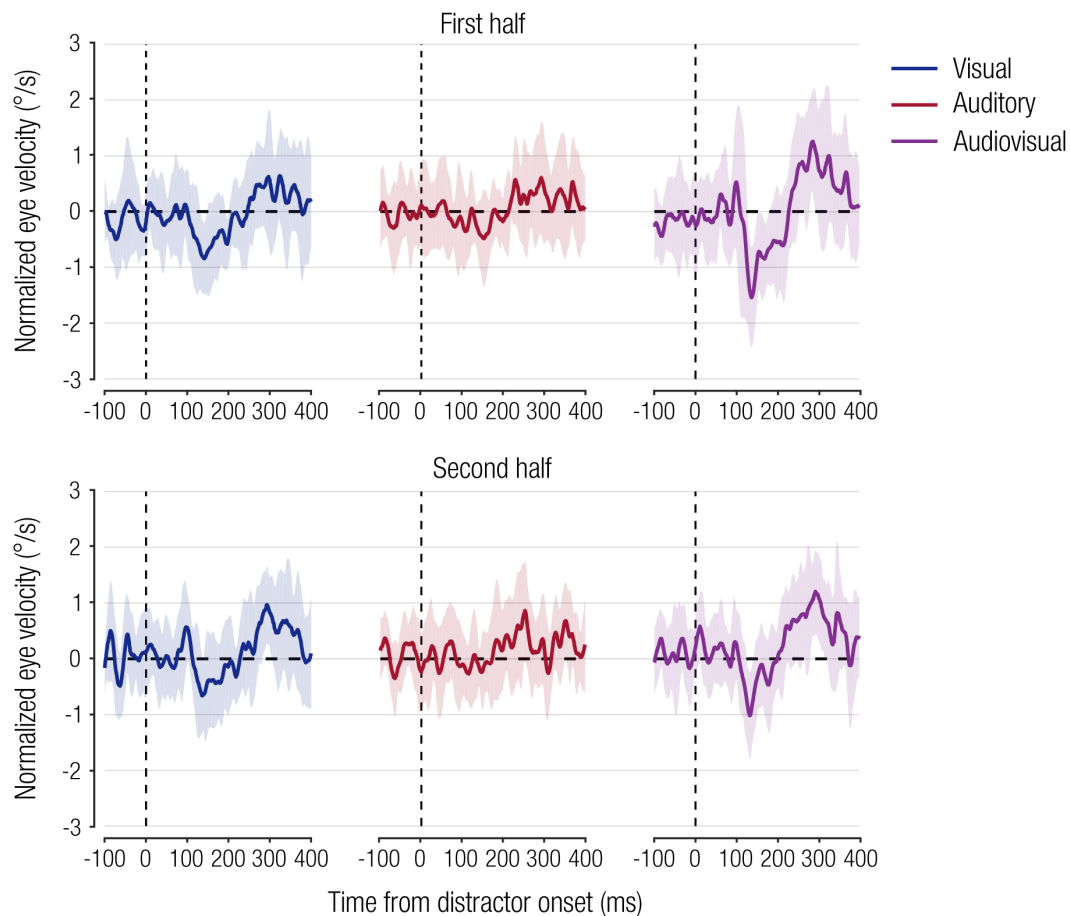


Figure 10. Control analysis showing data from Experiment 1 split between the first (upper panel) and second halves (lower panel) of the experiment. Bold lines represent means across observers and shaded areas represent  $\pm 1$  SD.

Whereas saccades are discrete events that are often completely inhibited in response to either visual or auditory distractors, smooth pursuit eye movements are continuous and provide a gradual measurement of distractor-evoked oculomotor inhibition. Pursuit inhibition allowed us to explore the mechanism of multisensory processing for oculomotor inhibition. We show that the multisensory response enhancement magnitude was equal to the linear sum of the responses evoked by the component stimuli. This additive signal combination was observed across visual contrast levels, indicating that additive multisensory response enhancement affects oculomotor inhibition across suprathreshold contrast levels.

Our findings are in line with previous studies showing effects of multisensory response enhancement on the latency of saccades (e.g., Corneil et al., 2002; Bell et al., 2005; Wang et al., 2017) or the latency and magnitude of pupil responses (Rigato et al., 2016; Wang et al., 2017; Van der Stoep et al., 2021). Wang and colleagues (2017) observed significantly stronger microsaccadic inhibition to audiovisual stimuli, as compared to visual or auditory stimuli, but this study did not distinguish

between additive and superadditive multisensory enhancement. Here we provide new evidence for an additive effect of multisensory response enhancement for rapid oculomotor inhibition.

The sensitivity to sensory stimuli typically decreases with repeated exposure to the same stimuli. To assess whether distractor-induced oculomotor inhibition decreased over the course of the experiment, we performed an additional control analysis.

In Figure 10, we re-plotted the data from Experiment 1 (see Figure 3A) separately for the first and second halves of the experiment. This analysis shows that the distractor-induced pursuit inhibition was stronger during the first half of the experiment, compared to the second half (compare upper and lower panels in Figure 10). However, the overall pattern remained similar during the course of the experiment, indicating the robustness of pursuit inhibition in response to the different distractors.

Overall, our results show that cross-modal stimuli affect eye movements at very short latencies, a finding that would be more difficult to establish with discrete behaviors such as saccades and button

presses, which typically have latencies of more than 200 ms. These results suggest that information from the two senses might converge earlier and more quickly to control behavior than previously thought.

### Additive multisensory integration in orienting behavior

Both additive and superadditive multisensory responses indicate the use of signals across modalities. Yet, some consider only superadditive effects conclusive behavioral evidence for the actual integration of signals due to involvement of non-linear signal combinations that cannot be explained by independent sensory processes alone (Stevenson et al., 2014). Following this logic, additive effects could also result from statistical facilitation of two separate sensory processes and might not necessarily require multisensory convergence and integration at the single neuron level. Human behavioral and neurophysiological studies on multisensory response enhancement have therefore focused primarily on superadditive combinations of multisensory stimuli. This emphasis on superadditive effects was initially supported by single-cell recordings showing firing rates to cross-modal stimuli that far exceed the linear sum of neural activity caused by the component stimuli (Meredith & Stein, 1983). However, subsequent studies demonstrate that superadditive multisensory enhancement is primarily observed when combining subthreshold or near-threshold unimodal stimuli (Stanford et al., 2005). With increasing stimulus strength, most neurons exhibit firing rates that approximate the linear sum of unimodal influences (Stanford & Stein, 2007).

These findings suggest that superadditivity is only a special case, rather than a hallmark, of multisensory integration that occurs when probed with near-threshold stimuli. In fact, the strict focus on superadditivity has been challenged (Stanford & Stein, 2007; Angelaki, Gu, & DeAngelis, 2009). Additive and even subadditive operations are common neural mechanisms of multisensory integration when tested with suprathreshold stimuli (Angelaki et al., 2009). Although we did not systematically assess observers' perceptual thresholds, all stimuli used in our experiments were designed to be well above perceptual thresholds. Our findings of additive multisensory enhancement are therefore in line with the idea of additive multisensory integration when probed with suprathreshold stimuli. Future studies could use a wider range of stimulus strength, including near and subthreshold unimodal stimuli, to probe whether stronger multisensory enhancement is observed when using weaker stimuli.

### Common mechanism for pursuit and saccade inhibition?

Our results, together with the results of two previous studies (Buonocore et al., 2019; Ziv & Bonneh, 2021), suggest a common inhibitory mechanism for pursuit and saccades, causing the eyes to rapidly freeze, or slow down, in response to the sudden onset of a salient event. Our results extend these findings showing that pursuit and saccade inhibition are stronger in response to cross-modal as compared to unimodal stimuli. Because oculomotor inhibition simultaneously affects pursuit and saccades, the catch-up saccade system cannot compensate for position and velocity errors accumulating due to low-velocity pursuit, as it normally does (De Brouwer et al., 2002). Interestingly, both systems are also aligned in their recovery from inhibition, as evidenced by similarities in magnitude and latency of the rebound response.

Due to their short latency, both pursuit and (micro-)saccadic inhibition may be mediated by a fast, subcortical pathway (Hafed, Yoshida, Tian, Buonocore, 2021; Buonocore & Hafed, 2023). Previous studies suggested a critical role of the SC in mediating (micro)saccadic inhibition (Engbert, 2006). The SC also plays a key role in the integration of cross-modal signals (Meredith & Stein, 1983; Stein & Stanford, 2008) and the coordination of various aspects of the oculomotor orienting response, such as head movements, saccades, and pupil response (Sparks, 1986; Corneil & Munoz, 2014). Although smooth pursuit is primarily driven by sensory signals in motion-sensitive middle temporal visual area (Lisberger & Movshon, 1999), the SC also encodes visual saliency during smooth pursuit eye movements (White, Itti, & Munoz, 2021), making it a candidate to mediate distractor-induced pursuit modulations. Recent neurophysiological findings question a causal role of the SC in mediating oculomotor inhibition and instead point to omnipause neurons (OPN) in the brainstem (Hafed et al., 2021; Buonocore & Hafed, 2023). Tonically firing OPNs prevents unintended saccades by inhibiting premotor saccadic burst neurons (Sparks, 2002). The same inhibitory mechanism has also been suggested for smooth pursuit eye movements (Missal & Keller, 2002; Krauzlis, 2004). Therefore OPNs are another possible candidate mediating inhibitory effects observed across different types of eye movements. However, whether and how OPNs respond to cross-modal stimuli is currently unknown.

Whereas our results and other behavioral and neurophysiological studies suggest a common mechanism controlling pursuit and saccadic inhibition, we also observed some noteworthy differences. First, the saccade inhibition was larger than pursuit inhibition: peak pursuit inhibition was ~10% of baseline pursuit velocity, but saccade rates decreased by ~70% and even

dropped to zero in some observers. Second, auditory distractors elicited weak pursuit inhibition (Figure 3) but strong inhibition of catch-up saccade rates (Figure 4). This difference indicates that pursuit eye movements might be less affected by auditory signals (Kerzel et al., 2010), congruent with the observation that humans have limited ability to smoothly track non-visual motion signals (Berryhill, Chiu, & Hughes, 2006). Future studies using larger sample sizes could assess whether inhibition magnitudes are correlated between pursuit and catch-up saccade rates across observers to provide further evidence for a common inhibition mechanism between the two types of eye movements.

When presenting moving visual distractors, smooth pursuit eye movements typically follow the vector average of distractor and target motion (Lisberger & Ferrera, 1997; Spering, Gegenfurtner, & Kerzel, 2006). Similarly, tracking a target in front of a stationary textured background causes retinal motion in the opposite direction of smooth pursuit and results in decreased eye velocity (Keller & Khan, 1986, Kimmig, Miles, & Schwarz, 1992, Mormann & Thier, 1995; Spering & Gegenfurtner, 2007; Kreyenmeier, Fooker, & Spering, 2017; Schröder, Keidel, Trautner, Radbruch, & Ettinger, 2022; for a review see Spering & Gegenfurtner, 2008). In our study, the visual distractor consisted of a stationary horizontally-oriented sinusoidal grating that does not cause any more retinal motion in the opposite direction of smooth pursuit than the frame of the computer monitor. It is therefore unlikely that the known effect of stationary textured backgrounds on smooth pursuit contributed to pursuit inhibition in the current study.

## Conclusions

Combining sensory inputs from different modalities is a vital capability resulting in increased response magnitudes, decreased reaction times, and lower detection thresholds, enabling more efficient reactions to a changing environment. The ability to rapidly detect and respond to changes extends to distractors—interfering and task-irrelevant events that must be suppressed. Here we provide new evidence for an additive effect of cross-modal signals on the magnitude of short-latency smooth pursuit inhibition, occurring reflexively to sudden-onset distractors. Due to the continuous nature of pursuit, its inhibition can provide a testbed to examine distractor suppression (Spering et al., 2006; Wöstmann et al., 2022) and a trial-by-trial window into short-latency multisensory processing.

*Keywords:* oculomotor inhibition, smooth pursuit, saccades, cross-modal integration

## Acknowledgments

The authors thank Alex L. White for help with the catch-up saccade rate analyses and members of the Spering lab for comments on an earlier version of the manuscript. This study was preregistered on the Open Science Framework (<https://osf.io/yc3w6>).

Commercial relationships: none.

Corresponding author: Philipp Kreyenmeier.

Email: philipp.kreyenmeier@gmail.com.

Address: Oculomotor Laboratory, UBC Hospital Koerner Pavilion, Vancouver, British Columbia, Canada.

\*HMC and MS should be considered joint senior authors. Each senior author will list this article with their name as senior author on their publication track record.

## References

- Abdi, H. (2007). Bonferroni test. In N. J. Salkind (Ed.), *Encyclopedia of measurement and statistics*, Vol. 1 (pp. 103–107). Thousand Oaks, CA: Sage.
- Abeles, D., Amit, R., Tal-Perry, N., Carrasco, M., & Yuval-Greenberg, S. (2020). Oculomotor inhibition precedes temporally expected auditory targets. *Nature Communication*, *11*, 3524, <https://doi.org/10.1038/s41467-020-17158-9>.
- Allen, K. M., Lawlor, J., Salles, A., & Moss, C. F. (2021). Orienting our view of the superior colliculus: Specialization and general functions. *Current Opinion in Neurobiology*, *71*, 119–126, <https://doi.org/10.1016/j.conb.2021.10.005>.
- Angelaki, D. E., Gu, Y., & DeAngelis, G. C. (2009). Multisensory integration: Psychophysics, neurophysiology, and computation. *Current Opinion in Neurobiology*, *19*, 452–458, <https://doi.org/10.1016/j.conb.2009.06.008>.
- Bell, A. H., Meredith, M. A., Van Opstal, A. J., & Munoz, D. P. (2005). Crossmodal integration in the primate superior colliculus underlying the preparation and initiation of saccadic eye movements. *Journal of Neurophysiology*, *93*, 3659–3673, <https://doi.org/10.1152/jn.01214.2004>.
- Berryhill, M. E., Chiu, T., & Hughes, H. C. (2006). Smooth pursuit of nonvisual motion. *Journal of Neurophysiology*, *96*, 461–464, <https://doi.org/10.1152/jn.00152.2006>.
- Buonocore, A., & Hamed, Z. M. (2023). The inevitability of visual interruption. *Journal of Neurophysiology*, *130*, 225–237.

- Buonocore, A., Skinner, J., & Hafed, Z. M. (2019). Eye-position error influence over “open-loop” smooth pursuit initiation. *Journal of Neuroscience*, *39*(14), 2709–2721, <https://doi.org/10.1523/JNEUROSCI.2178-18.2019>.
- Corneil, B. D., Van Wanrooij, M., Munoz, D. P., & Van Opstal, A. J. (2002). Auditory-visual interactions subserving goal-directed saccades in a complex scene. *Journal of Neurophysiology*, *88*(1), 438–54, <https://doi.org/10.1152/jn.2002.88.1.438>.
- Corneil, B. D., & Munoz, D. P. (2014). Overt responses during covert orienting. *Neuron*, *82*(6), 1230–1243, <http://dx.doi.org/10.1016/j.neuron.2014.05.040>.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*, 613–617, <https://doi.org/10.3758/BF03195489>.
- De Brouwer, S., Yuksel, D., Blohm, G., Missal, M., & Lefevre, P. (2002). What triggers catch-up saccades during visual tracking? *Journal of Neurophysiology*, *87*, 1646–1650, <https://doi.org/10.1152/jn.00432.2001>.
- Diederich, A., & Colonius, H. (2004). Bimodal and trimodal multisensory enhancement: Effects of stimulus onset and intensity on reaction time. *Perception & Psychophysics*, *66*(8), 1388–1404, <https://doi.org/10.3758/BF03195006>.
- Engbert, R. (2006). Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research*, *154*, 177–192, [https://doi.org/10.1016/S0079-6123\(06\)54009-9](https://doi.org/10.1016/S0079-6123(06)54009-9).
- Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research*, *43*, 1035–1045, [https://doi.org/10.1016/S0042-6989\(03\)00084-1](https://doi.org/10.1016/S0042-6989(03)00084-1).
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G\*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavioral Research Methods*, *39*(2), 175–191, <https://doi.org/10.3758/bf03193146>.
- Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, *16*(3), 553–610, <https://doi.org/10.1017/S0140525X00031575>.
- Frens, M. A., Van Opstal, A. J., & Van der Willigen, R. F. (1995). Spatial and temporal factors determine auditory-visual interactions in human saccadic eye movements. *Perception & Psychophysics*, *57*(6), 802–816, <https://doi.org/10.3758/bf03206796>.
- Gellman, R. S., Carl, J. R., & Miles, F. A. (1990). Short-latency ocular-following responses in man. *Visual Neuroscience*, *5*(2), 107–122, <https://doi.org/10.1017/s095252380000158>.
- Goettker, A., & Gegenfurtner, K. R. (2021). A change in perspective: The interaction of saccadic and pursuit eye movements in oculomotor control and perception. *Vision Research*, *188*, 283–296, <https://doi.org/10.1016/j.visres.2021.08.004>.
- Grenzbach, J., Wegner, T. G. G., Einhäuser, W., & Bendixen, A. (2021). Pupillometry in auditory multistability. *PLoS ONE*, *16*(6): e0252370, <https://doi.org/10.1371/journal.pone.0252370>.
- Hafed, Z. M., & Ignashchenkova, A. (2013). On the dissociation between microsaccade rate and direction after peripheral cues: Microsaccadic inhibition revisited. *Journal of Neuroscience*, *33*(41), 16220–16235, <https://doi.org/10.1523/JNEUROSCI.2240-13.2013>.
- Hafed, Z. M., Yoshida, M., Tian, X., Buonocore, A., & Malevich, T. (2021). Dissociable cortical and subcortical mechanisms for mediating the influences of visual cues on microsaccadic eye movements. *Frontiers in Neural Circuits*, *15*, 638429, <https://doi.org/10.3389/fncir.2021.638429>.
- Jeffreys, H. (1961). *Theory of Probability*. Oxford, UK: Oxford University Press.
- Keller, E. L., & Khan, N. S. (1986). Smooth-pursuit initiation in the presence of a textured background in monkey. *Vision Research*, *26*(6), 943–955, [https://doi.org/10.1016/0042-6989\(86\)90152-5](https://doi.org/10.1016/0042-6989(86)90152-5).
- Kerzel, D., Born, S., & Souto, D. (2010). Inhibition of steady-state smooth pursuit and catch-up saccades by abrupt visual and auditory onsets. *Journal of Neurophysiology*, *104*(5), 2573–2585, <https://doi.org/10.1152/jn.00193.2010>.
- Keyesers, C., Gazzola, V., & Wagenmakers, E. J. (2020). Using Bayes factor hypothesis testing in neuroscience to establish evidence of absence. *Nature Neuroscience*, *23*, 788–799, <https://doi.org/10.1038/s41593-020-0660-4>.
- Kimmig, H. G., Miles, F. A., & Schwarz, U. (1992). Effects of stationary textured backgrounds on the initiation of pursuit eye movements in monkeys. *Journal of Neurophysiology*, *68*(6), 2147–2214, <https://doi.org/10.1152/jn.1992.68.6.2147>.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What’s new in psychtoolbox-3. *Perception*, *36*(14), 1–16.
- Kozak, R. A., Kreyenmeier, P., Gu, C., Johnston, K., & Corneil, B. D. (2019). Stimulus-locked responses on human upper limb muscles and online-corrective reaches are preferentially evoked by low spatial frequencies. *eNeuro*, *6*(5), 1–17, <https://doi.org/10.1523/ENEURO.0301-19.2019>.

- Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology*, 91(2), 591–603, <https://doi.org/10.1152/jn.00801.2003>.
- Kreyenmeier, P., Fooker, J., & Sperling, M. (2017). Context effects on smooth pursuit and manual interception of a disappearing target. *Journal of Neurophysiology*, 118, 404–415, <https://doi.org/10.1152/jn.00217.2017>.
- Lisberger, S. G., & Ferrera, V. P. (1997). Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *Journal of Neuroscience*, 17(19), 7490–502, <https://doi.org/10.1523/JNEUROSCI.17-19-07490.1997>.
- Lisberger, S. G., & Movshon, J. A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *Journal of Neuroscience*, 19(6), 2224–2246, <https://doi.org/10.1523/JNEUROSCI.19-06-02224.1999>.
- Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique*. Cambridge, MA: MIT Press.
- Meredith, M. A., & Stein, B. E. (1983). Interactions among converging sensory inputs in the superior colliculus. *Science*, 221, 389–391, <https://doi.org/10.1126/science.6867718>.
- Miles, F. A., Kawano, K., & Optican, L. M. (1986). Short-latency ocular following responses of monkey. I. Dependence on temporospatial properties of visual input. *Journal of Neurophysiology*, 56(5), 1321–1354, <https://doi.org/10.1152/jn.1986.56.5.1321>.
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, 35(1), 99–115, <https://doi.org/10.1111/1469-8986.3510099>.
- Missal, M., & Keller, E. L. (2002). Common inhibitory mechanism for saccades and smooth pursuit eye movements. *Journal of Neurophysiology*, 88(4), 1880–1892, <https://doi.org/10.1152/jn.2002.88.4.1880>.
- Mohrmann, H., & Thier, P. (1995). The influence of structured visual backgrounds on smooth-pursuit initiation, steady-state pursuit and smooth-pursuit termination. *Biological Cybernetics*, 73(1), 83–93, <https://doi.org/10.1007/BF00199058>.
- Orban de Xivry, J. J., & Lefevre, P. (2007). Saccades and pursuit: Two outcomes of a single sensorimotor process. *Journal of Physiology*, 584(1), 11–23, <https://doi.org/10.1113/jphysiol.2007.139881>.
- R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing, <https://www.R-project.org>.
- Rigato, S., Rieger, G., & Romei, V. (2016). Multisensory signalling enhances pupil dilation. *Scientific Reports*, 6, 26188, <https://doi.org/10.1038/srep26188>.
- Rolfs, M., Kliegl, R., & Engbert, R. (2008). Toward a model of microsaccade generation: The case of microsaccadic inhibition. *Journal of Vision*, 8(11), 5, <https://doi.org/10.1167/8.11.5>.
- Rowland, B. A., Quessy, S., Stanford, T. R., & Stein, B. E. (2007). Multisensory integration shortens physiological response latencies. *Journal of Neuroscience*, 27(22), 5879–5884, <https://doi.org/10.1523/JNEUROSCI.4986-06.2007>.
- Schröder, R., Keidel, K., Trautner, P., Radbruch, A., & Ettinger, U. (2022). Neural mechanisms of background and velocity effects in smooth pursuit eye movements. *Human Brain Mapping*, 44, 1002–1018, <https://doi.org/10.1002/hbm.26127>.
- Sparks, D. L. (1986). Translation of sensory signals into commands for control of saccadic eye movements: Role of primate superior colliculus. *Physiological Reviews*, 66(1), 118–171, <https://doi.org/10.1152/physrev.1986.66.1.118>.
- Sparks, D. L. (2002). The brainstem control of saccadic eye movements. *Nature Reviews Neuroscience*, 3, 952–964, <https://doi.org/10.1038/nrn986>.
- Sperling, M., & Gegenfurtner, K. R. (2007). Contextual effects on smooth-pursuit eye movements. *Journal of Neurophysiology*, 97, 1353–1367, <https://doi.org/10.1152/jn.01087.2006>.
- Sperling, M., & Gegenfurtner, K. R. (2008). Contextual effects on motion perception and smooth pursuit eye movements. *Brain Research*, 1225, 76–85, <https://doi.org/10.1016/j.brainres.2008.04.061>.
- Sperling, M., Gegenfurtner, K. R., & Kerzel, D. (2006). Distractor interference during smooth pursuit eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 1136–1154, <https://doi.org/10.1037/0096-1523.32.5.1136>.
- Stanford, T. R., & Stein, B. E. (2007). Superadditivity in multisensory integration: Putting the computation in context. *Neuroreport*, 18(8), 787–792, <https://doi.org/10.1097/WNR.0b013e3280c1e315>.
- Stanford, T. R., Quessy, S., & Stein, B. E. (2005). Evaluating the operations underlying multisensory integration in the cat superior colliculus. *Journal of Neuroscience*, 25(28), 6499–6508, <https://doi.org/10.1523/JNEUROSCI.5095-04.2005>.
- Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, 9, 255–266, <https://doi.org/10.1038/nrn2331>.
- Stevenson, R. A., Ghose, D., Fister, J. K., Sarko, D. K., Altieri, N. A., Nidiffer, A. R., ... Wallace, M. T. (2014). Identifying and



- quantifying multisensory integration: A tutorial review. *Brain Topography*, 27(6), 707–730, <https://doi.org/10.1007/s10548-014-0365-7>.
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, 38(5), 816–827, <https://doi.org/10.1111/1469-8986.3850816>.
- Van der Stoep, N., Van der Smagt, M. J., Notaro, C., Spock, Z., & Naber, M. (2021). The additive nature of the human multisensory evoked pupil response. *Scientific Reports*, 11, 707, <https://doi.org/10.1038/s41598-020-80286-1>.
- Wang, C. A., Blohm, G., Huang, J., Boehnke, S. E., & Munoz, D. P. (2017). Multisensory integration in orienting behavior: Pupil size, microsaccades, and saccades. *Biological Psychology*, 129, 36–44, <https://doi.org/10.1016/j.biopsycho.2017.07.024>.
- White, A. L., & Rolfs, M. (2016). Oculomotor inhibition covaries with conscious detection. *Journal of Neurophysiology*, 116, 1507–1521, <https://doi.org/10.1152/jn.00268.2016>.
- White, B. J., Itti, L., & Munoz, D. P. (2021). Superior colliculus encodes visual saliency during smooth pursuit eye movements. *European Journal of Neuroscience*, 54(1), 4258–4268, <https://doi.org/10.1111/ejn.14432>.
- Widmann, A., Engbert, R., & Schröger, E., (2014). Microsaccadic responses indicate fast categorization approach to study auditory cognition. *Journal of Neuroscience*, 34(33), 11152–11158, <https://doi.org/10.1523/JNEUROSCI.1568-14.2014>.
- Wöstmann, M., Störmer, V. S., Obleser, J., Addleman, D. A., Andersen, S. K., Gaspelin, N., . . . Theeuwes, J. (2022) Ten simple rules to study distractor suppression. *Progress in Neurobiology*, 213, 102269, <https://doi.org/10.1016/j.pneurobio.2022.102269>.
- Ziv, I., & Bonneh, Y. S. (2021). Oculomotor inhibition during smooth pursuit and its dependence on contrast sensitivity. *Journal of Vision*, 21(2), 12, <https://doi.org/10.1167/jov.21.2.12>.