Authors' note

This is the post-print version of the following article : Geers, L., Doré-Mazars, K., & Andres, M. (2025). The time-dependent modulation of saccade amplitude by illusory length reflects a shared representation between perception and action. *Journal of Experimental Psychology: Human Perception and Performance*, 10.1037/xhp0001382. This is the version after peer review and acceptance but before the publisher's final copyediting and formatting. The final autorithative version is available online at : https://doi.org/10.1037/xhp0001382

The time-dependent modulation of saccade amplitude by illusory length reflects a shared representation between perception and action

Authors

Laurie Geers[1,2], Karine Doré-Mazars[3] & Michael Andres[1,2]

Affiliations

[1] UCLouvain, Psychological Science Research Institute, Belgium

[2] UCLouvain, Institute of Neuroscience (IoNS), NEUR division, Belgium

[3] Université Paris Cité, Vision Action Cognition, Boulogne-Billancourt, France

Emails

laurie.geers@uclouvain.be

karine.dore@parisdescartes.fr

michael.andres@uclouvain.be

Word count: 9,652

Abstract

Are eye movements miscalibrated when the distance to be crossed is misperceived? The two-visual-stream hypothesis posits that while perception is influenced by visual context and thus prone to illusions, actions rely on context-independent metrics and are thus unaffected by such distortions. In contrast, empirical evidence consistently shows that saccadic eye movements are influenced by the Müller-Lyer illusion. However, this finding could be explained by saccades being attracted toward the figure's center of gravity, while perceptual distortion would result from distinct mechanisms. To disentangle these effects, we conducted four experiments (N = 114) between 2022 and 2025, measuring the amplitude of saccades performed along horizontal lines embedded in Müller-Lyer figures carefully designed to control for center-of-gravity biases. Results showed that both saccade amplitude and length judgment were systematically modulated by the illusion beyond what could be attributed to changes in the actual center of gravity, its saliency or computation time. Additionally, the illusion's influence on saccade amplitude diminished after a longer previewing time (2,000 ms) compared to a shorter one (50 ms). These findings support the hypothesis that perception and oculomotor behavior rely on a shared visual representation that is influenced by contextual information but becomes more precise with increased processing time.

Key-words: perception-action model, center-of-gravity effect, visual illusion, size processing, time scale

Public significance statements

- Saccadic eye movements are affected by the visual illusion of Müller-Lyer.
- The illusion effect on saccade amplitude is reduced when the observer has more time to process the stimulus.
- The illusion effect is not the same as the effect of the stimulus's center of gravity on the endpoint of the saccade.
- These results demonstrate that oculomotor behavior and perception rely on a shared visual representation improving over time.

I. Introduction

The interplay between perception and oculomotor behavior is complex. Eye movements are instrumental to visual scene exploration but, at the same time, having an integrated perception of the visual scene is useful for coordinating oculomotor behavior (Yarbus, 1967). A negative consequence of such interplay is that perception might occasionally deceive eye movements. If the distance crossed by the eyes is misperceived, a logical prediction is that the saccade amplitude will also be miscalibrated. It has been proposed, however, that oculomotor behavior might be resistant to perceptual errors because the visual processes underlying perception and action would be partly independent (Goodale & Milner, 1992; Milner & Goodale, 2006).

The two visual streams hypothesis assumes that the visual system is divided into two streams that give a different weight to the visual context in the computation of object metrics to meet the specific requirements of perception and action. Specifically, the ventral stream would process object properties, such as their size and distance, relative to the surrounding objects, from an allocentric perspective, to form a stable representation of the visual world allowing *inter alia* object recognition. In contrast, the dorsal stream would process size and distance from an egocentric perspective, without taking into account surrounding objects, to allow accurate actions (Goodale & Milner, 1992; Milner & Goodale, 2006). Visual illusions provide paradigmatic examples of the influence of visual context on perception, hence providing a test of the relative independence of size estimation for actions performed in a similar context. Because eye movements primarily rely on the dorsal visual stream (Munoz, 2002), they should escape visual illusions induced by the visual context. However, several

studies found that such illusions do influence saccadic eye movements. In the Müller-Lyer illusion (MLI), wings-in or wings-out arrows attached to a horizontal segment (i.e., <-> and >-<) make this segment appear shorter or longer, but they also affect saccades performed from one end of the horizontal segment to the other. Specifically, saccade amplitudes were shorter when performed on wings-in figures (<->) compared to wings-out (>-<) figures, mirroring the effect observed on perception (Bernardis et al., 2005; Binsted & Elliott, 1999; de Grave et al., 2006; Festinger et al., 1968). Although the magnitude of the illusion effect varies by 30% depending on the methodology, meta-analyses including over 20 experiments confirmed the existence of a consistent bias of the MLI on saccadic eye movements (Bruno et al., 2010; MacKeith & Knox, 2012).

The two-visual stream hypothesis also posits that vision-for-perception and vision-for-action operate with different temporal scales (Goodale & Milner, 1992; Milner & Goodale, 2006). Perceptual processing in the ventral stream would proceed relatively slowly to support the formation of stable, long-lasting representations. In contrast, the visuomotor system of the dorsal stream would rapidly compute object coordinates to guide action within a dynamic environment. However, these computations would be short-lived (a feature also referred to as 'dorsal amnesia'; Schenk & Hesse, 2018). Consequently, the dorsal stream would rely on current visual input, generating the necessary metrics only at the very moment an action is initiated, rather than maintaining continuously updated representations (Goodale & Milner, 1992; Westwood & Goodale, 2003). From this perspective, saccadic behavior should be unaffected by the previewing time of an object before performing a movement towards that object. In contrast, several studies have shown that the effect of the MLI on saccades decreases as the time available to view the illusion before initiating the movement

increases, mirroring the effects observed on perceptual judgments, which are also less influenced by the illusion with longer previewing times (De Grave & Bruno, 2010; de Brouwer et al., 2014; Medendorp et al., 2018; van Zoest & Hunt, 2011). Collectively, these findings challenge a functional dissociation between the perceptual and visuomotor pathways, suggesting instead that perception and action are underpinned by a shared visual representation that becomes more accurate over time (van Zoest & Hunt, 2011). This interpretation aligns with a growing body of literature questioning the predictions of the two-visual systems hypothesis (*e.g.*, de Haan et al., 2018; Geers et al., 2021; Rossetti et al., 2017).

However, an alternative interpretation has been proposed, preventing firm conclusions about the functional (di)similarity of perception and oculomotor behavior. According to this view, the miscalibration of saccades performed along the MLI would be due to a Center of Gravity (CoG) effect that operates independently of the mechanisms influencing the perception of the segment's length (Chen et al., 2020; de Grave et al., 2006; Gilster and Kuhtz-Buschbeck, 2010). The CoG effect refers to the tendency of saccades aimed at a target embedded in a configuration of multiple nearby visual elements to be biased towards the center of this configuration (Coren & Hoenig, 1972; Findlay, 1982). In the context of the MLI, this implies that saccades directed towards the tip of wings-in wings-out arrows might thus be respectively shorter and longer because they are attracted towards the CoG of the arrowhead. In this scenario, the CoG effect would mimic the perceptual bias but through independent processes that are unrelated to the represented length of the horizontal segment. Support for this view comes from studies that attempted to minimize perceptual distortions, for example by detaching the arrowheads from the horizontal segment. These studies found that the typical saccadic bias associated with the MLI persisted despite reduced

perceptual distortion (Chen et al., 2020; Gilster & Kuhtz-Buschbeck, 2010). Furthermore, research has demonstrated that the influence of the CoG effect diminishes with longer saccadic latencies (Coëffé & O'Regan, 1987), which may account for the observed reduction in the MLI effect over time. The finding of a CoG effect biasing saccade amplitude in the same direction and with the same course as length distortion raises uncertainty about the nature of previously reported effects. It is currently unclear whether the visual illusion may affect saccade amplitude beyond the CoG effect as previous studies have failed to fully disentangle the two effects.

This study investigated the impact of the MLI on saccadic eye movements and its modulation by previewing time while controlling for the CoG effect. To do so, we systematically varied the amplitude of the angle formed by the arrows of MLI figures, while keeping the horizontal projection of the fins of the arrow constant. Previous research has shown that sharper angles amplify the perceptual distortion, causing greater underestimation (wings-in) or overestimation (wings-out) of the horizontal segment length (Weidner & Fink, 2007). By holding the horizontal projection of the fins constant, we ensured a stable CoG across different angles pointing in the same direction, allowing us to isolate the effect of the illusion from any influence of the CoG. Experiment I aimed to validate this modified version of the MLI from a perceptual point of view. In particular, we verified that similar distortions are observed in perceptual judgements when horizontal projection is controlled and when it is not. We expected sharper angles to induce a stronger illusion effect in both cases. Experiment II aimed to test whether the MLI figures with a constant fin projection influence the amplitude of saccades made along the horizontal segment, in a way that parallels their effect on perceptual judgments. The two visual streams hypothesis

predicts no parametric modulation of saccade amplitude across angles pointing in the same direction but a stepwise difference between wings-in and wings-out configurations due to a possible CoG effect. Alternatively, if a single visual representation underlies both saccades and perception, we expect a linear increase of a saccade amplitude as the angle increases, even within wings-in and wings-out configurations. Experiment III aimed to exclude that differences across angles sharing the same CoG could be attributed to the CoG of shallower angles requiring more time to be computed, due to the reduced salience of the arrowhead's illusory contour. Finally, Experiment IV investigated whether the illusion effect differs between short (50 ms) and long (2,000 ms) previewing times, while controlling for the CoG. If the illusion effect on saccades reflects a shared visual representation for perception and action that becomes more accurate over time, we would expect a smaller effect after the long previewing time than the short previewing time, even across angles that share the same CoG. Alternatively, the finding of a steady illusion effect over time, after controlling the CoG, would suggest that saccades are guided by a distinct visuomotor representation that emphasizes the visual input available at movement initiation, irrespective of the previewing time. Experiment IV is thus important to exclude that, in previous studies, the time course of illusion effects on saccadic behavior resulted from the decreasing influence of the CoG.

II. Transparency and Openness

We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the studies. The data of all experiments have been made publicly available on Open Science Framework (OSF) and can be accessed at https://osf.io/rkb8v. Data preprocessing and analyses were performed using R (version 4.2.1)

and R Studio software (2022.07.1). Plots were generated using the *ggplot2* package. The study design and analyses were not pre-registered.

III. Experiment I

3.1. Methods

3.1.1. Participants

Twenty-eight Caucasian students (24 females and 4 males; M_{age} = 21 years, SD_{age} = 5 years) from the Université Catholique de Louvain, Belgium, participated in this study during November 2022. They all reported having normal or corrected-to-normal vision and had no known neurological or oculomotor deficits. The sample size was determined through a sample size analysis conducted in G*Power indicating that at least 26 participants were needed to detect an effect of angle with an average effect size considered practically relevant (Cohen's f^2 = .20; Open Science Collaboration, 2015) in a repeated-measures one-way ANOVA with 7 levels, a standard power criterion of .80, and an alpha level of 0.05. This decision also aligns with previous research, which typically employed sample sizes around 20 participants (Bruno et al., 2010). The study was non-invasive, performed following the APA ethical standards, and approved by the Biomedical Ethical Committee of the Université catholique de Louvain (B4032021000130).

3.1.2. Apparatus and Stimuli

Participants were seated at 57 cm from a LCD monitor (dimensions: 52.8 x 29.9 cm; resolution: 1920 x 1080 pixels; refresh rate: 60Hz). The stimuli consisted of MLI configurations displayed in black on a grey background. We employed seven distinct angles

between the horizontal segment and the fins of the arrows, ranging from -67.5° to + 67.5° relative to the vertical axis in 22.5° increments. Negative angles corresponded to wings-in configurations, positive angles corresponded to wings-out configuration and the 0° angle corresponded to a neutral configuration with vertical bars not inducing any illusion. Each angle was presented in two variants: one maintaining the length of the fins at 1.5° of visual angle across angles (Figure 2A), and another maintaining the horizontal projection of the fins at 1.5° of visual angle across angles (Figure 2B). The variant with a constant fin length is the conventional one. In contrast, the variant with a constant fin projection allows the height of the triangle formed by the arrowhead, and thus the CoG, to remain constant across angles pointing in the same direction. Stimuli presentation was handled by PsychoPy 2023.2.1.

3.1.3. Task and Procedure

Participants had to reproduce the length of a previously seen horizontal reference line, presented without arrows, while the reproduced line was embedded within either the constant length or constant horizontal projection variant of the MLI described above (Figure 1). Each trial began with a fixation cross displayed at the center of the screen for 500 ms. Following this, the horizontal reference line, measuring either 4° or 5° of visual angle, was presented at the center of the screen for 2,000 ms. Afterwards, a visual noise mask appeared for 200 ms. Finally, a MLI configuration was displayed at the center of the screen, with the length of the horizontal segment randomly set to a value between 2° and 7° of visual angle. Participants adjusted the length of this horizontal segment using the arrow keys until it matched the previously seen reference line. No time constraints were imposed for this task. Once satisfied with their reproduction, participants pressed the space bar to proceed to the

next trial. Following 14 practice trials, participants completed two blocks of trials: one for the constant length variant and one for the constant projection variant. Each block comprised 224 trials, with the 14 possible combinations of angle and reference length being presented 16 times in a random order. The order of the blocks was counterbalanced across participants.

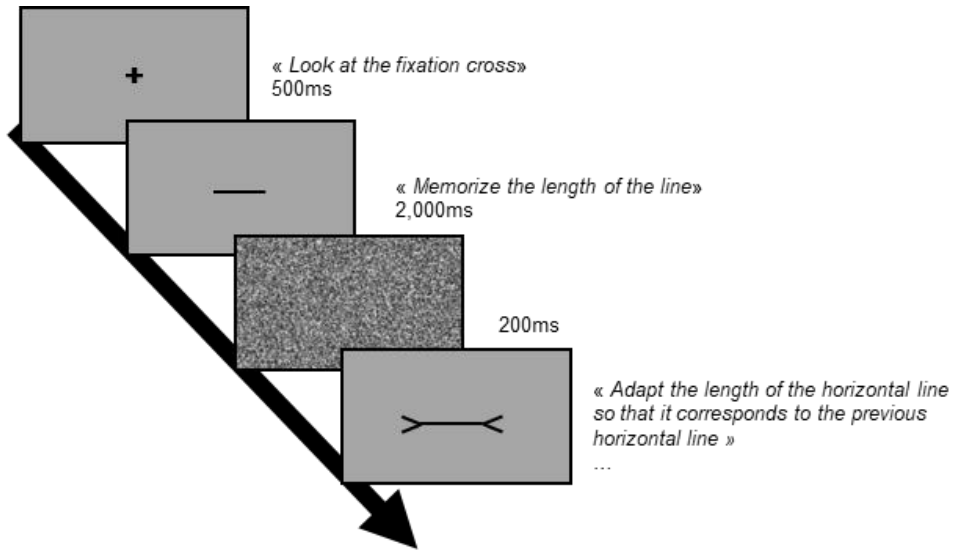


Figure 1. Schematic representation of the time course of the length reproduction task of Experiment I.

3.1.4. Data Analyses

Trials with a reaction time (RT) below 200 ms (0.03% of the data) or reproduced length exceeding 3 times the individual's median absolute deviation (MAD) for the concerned reference length and MLI variant (0.32% of the data; Leys et al., 2013) were excluded. After exclusions, the average reproduced length was 4.65° of visual angle (SE = 0.01°). Next, the perceptual bias introduced by the MLI in the reproduced length was computed for each trial. The bias was quantified as the ratio of the reproduced length to the reference's length using the following formula:

$$Bias = \frac{Reproduced\ Length - Reference's\ Length}{Reference's\ Length}\ x\ 100$$

Values close to zero indicate no bias, while negative and positive values reflect under- and over-reproduction of the reference's length, respectively. Computing the bias as a proportion of reference length serves to normalize the measure but does not necessarily make it independent of length. The reason for using two reference lengths in this study (4° or 5° of visual angle) was to ensure some variability in the responses but, as we had no theoretical interest in this factor, we did not include it in the statistical analysis and estimates thus pool the two reference lengths.

To examine the effect of the angle amplitude on this bias, we fitted a linear mixed model (LMM) separately for each MLI variant, with Angle (7 levels: -67.5°, -45°, -22.5°, 0°, +22.5°, +45°, +67.5°) as a categorical fixed effect and participant as a random intercept. Based on prior work (Weidner & Fink, 2007), we expected a gradual shift from a positive to a negative bias between angles -67.5° and +67.5° for both MLI variants. To be able to test whether the illusion affects saccades beyond the CoG in Experiment II, the length distortion had to be sufficiently large to produce at least one significant difference between angles pointing in the same direction (thus sharing the same CoG). To verify this condition, we performed Bonferroni-corrected pairwise planned contrasts between same-direction angles using the *emmeans* R package (Lenth et al., 2019).

To directly compare illusion strength across variants, we fitted a second LMM including the interaction between Angle (treated as continuous) and Variant (2 levels: constant length vs. projection) as fixed effect and participant as a random intercept. Including

the interaction term and coding Angle as a continuous variable allows comparing the slopes of the Angle effect, and thereby illusion strength, across MLI variants. Note that the goodness of fit could not be used to assess the superiority of the interaction model over the models computed separately for each variant of MLI because these models were specifically designed to make pairwise comparisons between angles, hence angle was coded as a categorical variable instead of a continuous variable. However, the interaction model was analyzed using the anova() function, which performs Type I sequential likelihood ratio tests to assess the relative contribution of each fixed effect, i.e. the main effects of Angle and Variant and their interaction. This aligns with a hierarchical model comparison approach.

The equivalent Bayesian analyses were also computed using the *brms* R package (Bürkner, 2017) to provide Bayes Factors (BF_{10}) ranging from 0 to ∞, where values below 1 indicate increasing evidence for the null hypothesis, and values above 1 indicate increasing evidence for the alternative hypothesis (H_1/H_0; Dienes, 2014). A *BF* greater than 3 is typically considered strong evidence in favor of the alternative hypothesis, while a *BF* less than 1/3 is considered strong evidence for the null hypothesis (Jeffreys, 1988).

3.2. Results

3.2.1. Constant-length Variant

The LMM on the bias in the reproduced length induced by the typical constant-length variant showed a significant main effect of Angle, $F(6, 6220) = 411.30$, $p < .001$, $\eta^2p = .28$, $BF_{10} = \infty$, indicating a progressive shift from +7.14 % (SE = 0.40 %) to -10.85 % (SE = 0.37 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values < .001; see detailed

statistics in Supplementary Table 1 of Appendix A), except between angles +45° and +67.5°, $t(6220) = 0.64$, $p = 1.000$ (Figure 2A).

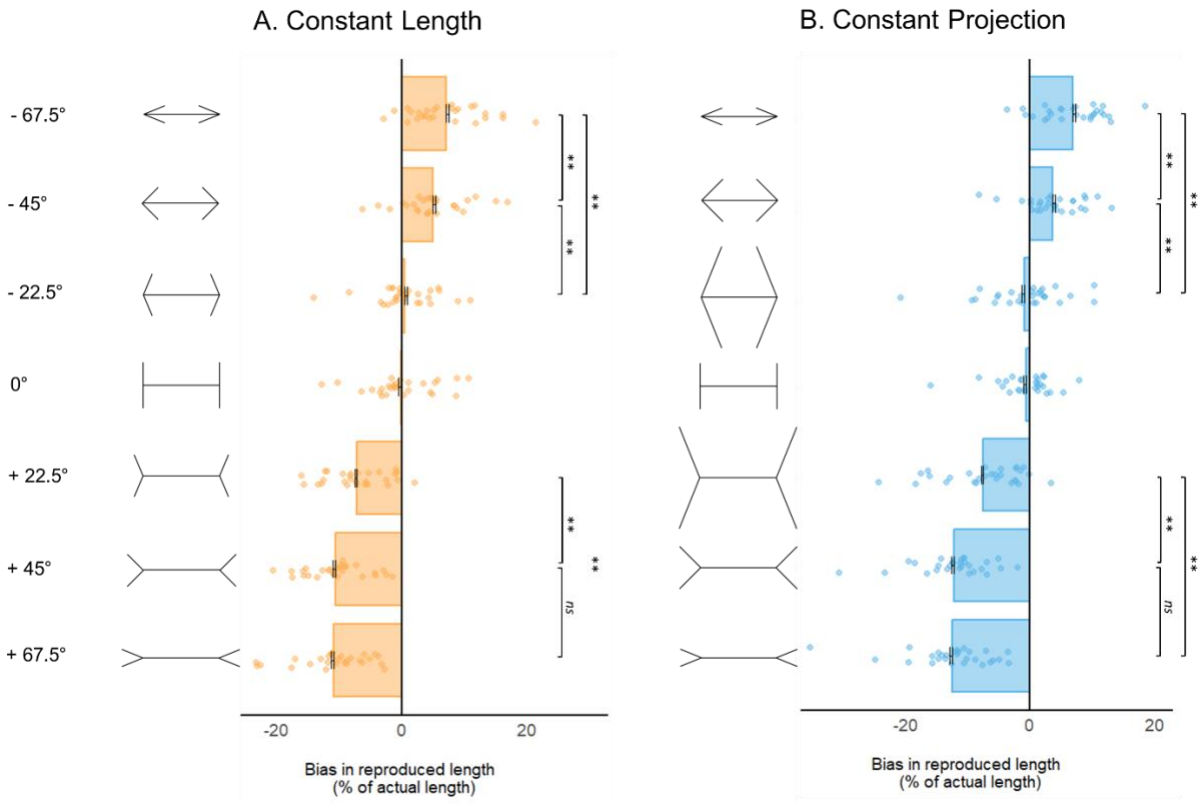


Figure 2. The [A] constant-length and [B] constant-projection variants of the Müller-Lyer illusion used in Experiment I with the bias they induced in the reproduction of the horizontal segment's length (in percentage of the actual length of the horizontal segment). Error bars represent the SE and dots represent the individual means. Note that while individual means are plotted, statistical analyses were conducted on single-trial data (using mixed-effects modeling).
** *p*-value < .01; *ns p-value > 0.05*.

3.2.2. Constant-projection Variant

The LMM on the bias induced by the constant-projection variant in the reproduced length also showed a significant main effect of Angle, $F(6, 6212) = 428.88$, $p < .001$, $\eta^2p = .29$, $BF_{10} = \infty$, indicating a progressive shift from +6.93 % (SE = 0.42 %) to -12.53 % (SE = 0.39 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values < .001; see

detailed statistics in Supplementary Table 1 of Appendix A), except between angles +45° and +67.5°, $t(6212) = 0.56$, $p = 1.000$ (Figure 2B).

3.2.3. Illusion Strength as a function of Variant

The LMM including the interaction between Angle and Variant showed a significant main effect of Angle, $F(1, 12469) = 4721.94$, $p < .001$, $\eta^2p = .27$, $BF_{10} = \infty$. The negative slope of the angle's effect (β = -0.15, $p < .001$) was consistent with the decrease found in the separate analyses. There was also a significant effect of Variant, $F(1, 12469) = 27.67$, $p < .001$, $\eta^2p < .01$, $BF_{10} = 13{,}348.33$, indicating that there was a greater underestimation of reproduced length when embedded in the constant-projection variant (M = –3.32 %, SE = 0.17 %) than in the constant-length variant (M = -2.28 %, SE = 0.17 %). Importantly, there was no significant Angle by Variant interaction, $F(1, 12469) = 2.40$, $p = .121$, $\eta^2p < .01$, $BF_{10} < 0.001$, providing strong evidence that the effect of angle, and thus illusion, was similar across variants.

IV. Experiment II

Experiment I demonstrated that the angle of the arrows in MLI figures effectively modulated the perceived length of the horizontal segment. Specifically, the perceived length of the replica embedded in the MLI was most underestimated for the wings-in configuration with the sharpest angle (and therefore reproduced longer than the reference's length). This underestimation gradually diminished as the angle amplitude increased, eventually transitioning to an overestimation for the wings-out configurations. It should be noted that the bias for the wings-out configurations was stronger than for the wings-in configurations. This asymmetry is consistent with the results of previous studies showing that expansion-

type illusions, including the MLI, typically produce stronger effects than their contraction counterparts (Christie, 1975; Piaget, 2013). Importantly, the modulation of perceived length was consistent across both the novel constant-projection variant—where the horizontal projection of the fins was held constant—and the more conventional MLI variant, where the fin length remains constant. Most crucially, the systematic modulation produced significant differences between angles pointing in the same direction and thus having the same CoG in both variants. Building on these results, we explored the effect of the constant-projection variant on saccadic eye movements. By maintaining a consistent CoG across angles pointing in the same direction, this variant allowed us to investigate whether the effect on saccades persists when controlling for the CoG. To do so, participants were asked to perform saccades along the horizontal segment of constant-projection MLI figures and, for direct comparison with perception, to complete a length reproduction task similar to that in Experiment I.

4.1. Methods

4.1.1. Participants

Thirty different Caucasian students from the Université catholique de Louvain, Belgium, participated in this study between March and July 2023. Two were excluded from data analyses due to poor-quality eye-tracking data (saccades were recorded in less than 60% on the trials), leaving 28 participants (25 females and 3 males; M_{age} = 22 years, SD_{age} = 4 years) in the final sample. To determine the required sample size, we first replicated the G*Power estimation used in Experiment I for the individual analyses. Additionally, we conducted simulation-based power analyses using the simr package in R, following the procedure outlined by Green and MacLeod (2015), to estimate the number of participants

needed to detect a small interaction effect between angle and task. We began by deriving the regression coefficient corresponding to an interaction effect size of η^2_p = .02. This was achieved by proportionally scaling the squared regression coefficients to match the ratio of η^2_p values based on the angle effect observed in Experiment I (β = 0.15, η^2_p = .28), resulting in an estimated interaction coefficient of β = 0.04. Simulations indicated that a sample of 4 participants would yield 80% power to detect this interaction using our design and analysis approach. Our final sample of 28 participants therefore provides ample power—achieving 100%—to detect the hypothesized interaction between angle and task.

4.1.2. Apparatus and Stimuli

Using a chinrest, the participant's head was maintained at a constant distance of 57 cm from an LCD monitor (dimensions: 37.6 x 21.2 cm, resolution: 1920 x 1080 pixels, refresh rate: 144Hz) throughout the experiment. We used the same constant-projection stimuli as used in Experiment I (Figure 2B), with the length of the horizontal segment being either 4 or 5° of visual angle. Movements of the dominant eye were recorded in a head-stabilized setting at a sample rate of 1,000 Hz using an Eyelink Portable Duo eye tracker (SR Research, Mississauga, ON, Canada; average accuracy range: 0.25° to 0.5°; gaze tracking range: 32° horizontally and 25° vertically). Before each experimental block, the eye tracker was calibrated to the screen using a built-in 5-point protocol.

4.1.3. Procedure

Each participant completed two tasks: a saccade task, where they performed a saccadic eye movement from one end of the horizontal segment of the MLI figure to the other, and the length reproduction task of Experiment I, which was adapted to match the saccade

task closely. In both tasks, a fixation cross appeared at the center of the screen for 1,500 ms, during which participants were encouraged to blink if needed. Following this, a red dot (0.2° of visual angle in diameter) was presented at the center of the screen for participants to fixate on. Once fixation was held for 200 ms, an MLI configuration appeared, with one end of the horizontal segment being aligned with the red dot and the other end extending to the left or right. Participants were instructed to maintain fixation on the red dot. After a random interval of 1.8 to 2.2 seconds, the red dot disappeared.

In the saccade task, the disappearance of the red dot served as the GO signal for participants to execute a saccade toward the opposite end of the horizontal segment while ignoring the attached arrows. After fixation was maintained on a point over the midpoint of the horizontal segment for 200 ms, the MLI configuration disappeared, and the next trial began.

In the length reproduction task, the MLI configuration and red dot disappeared simultaneously, followed by 200 ms of visual random noise. A single horizontal line without fins then appeared with one extremity at the center of the screen and the other extending in the same direction as the previous MLI configuration, with a random length between 2° and 7° of visual angle. Participants were instructed to adjust the length of this line using the arrow keys until it matched the horizontal segment of the preceding MLI configuration. No time pressure was imposed during this task. Once participants were satisfied with the reproduced length, they pressed the space bar to initiate the next trial.

Eye movements were recorded in both tasks, capturing data from the appearance of the red dot until the disappearance of the MLI configuration (Figure 3).

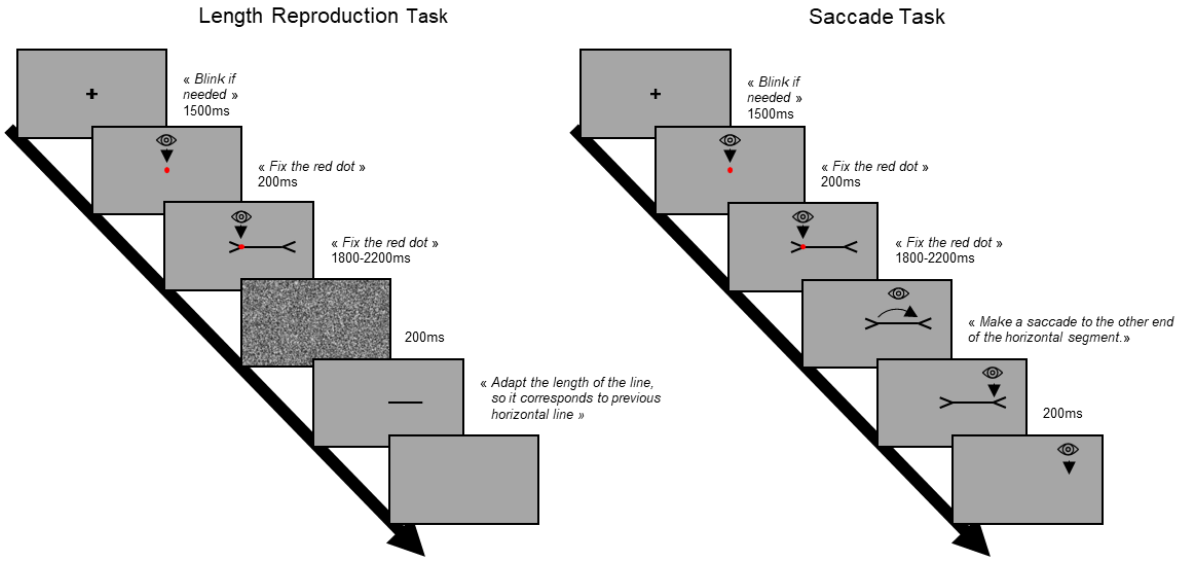


Figure 3. Schematic representation of the time course of the length reproduction and saccade tasks.

Before each task, participants underwent a training session in which they practiced the experimental task while receiving feedback if they made any eye movements before the red dot disappeared. The training session ended once the participant completed 15 trials without any unwanted eye movements. After the training, participants completed two blocks for each experimental task. Each block consisted of the 14 possible combinations of angle and horizontal segment length, randomly presented four times—twice for each direction (extending to the left or right). The order of the experimental tasks was counterbalanced across participants.

4.1.4. Data Analyses

Eyelink DataViewer (SR Research) was used to generate a saccade report, which included the starting and ending positions of each saccade along the x-axis, as well as its direction and latency. Saccade amplitudes were subsequently calculated from this report by taking the absolute difference between the starting and ending positions along the x-axis.

In the length reproduction task, the saccade report served to exclude trials where saccades of over half the length of the horizontal segment occurred during the presentation of the MLI configuration (5.22% of the data). Trials with reproduced lengths exceeding 3 times the individual's MAD for the concerned horizontal segment length and task (3.63% of the data; Leys et al., 2013) were also excluded. After these exclusions, average reproduced length was 4.39 ° of visual angle (SE = 0.02°). These remaining trials were used to compute the bias introduced by the MLI in the reproduced length as in Experiment I.

In the saccade task, we eliminated trials where no saccade covering more than half of the horizontal segment was detected during the trial (5.39 % of the trials). We also removed trials in which saccades of over half the horizontal segment occurred before the GO signal (0.99 % of the trials). Additionally, we excluded trials where saccade amplitude and/or latency exceeded 3 times the individual's MAD for the concerned horizontal segment length, angle amplitude, and variant (7.14 % of the data; Leys et al., 2013). After these exclusions, the average saccade amplitude was 4.05 ° of visual angle (SE = 0.02°) and average saccade latency was 339 msec (SE = 2 msec). We then calculated the bias introduced by the MLI on the saccade amplitude of the remaining trials ~~for each participant~~ following the same procedure as for the length reproduction task.

We conducted the same analyses as in Experiment I, except that Variant was replaced by Task (2 levels: reproduction vs. saccade). Regarding the separate analysis for the length reproduction task, we expected the same results as Experiment I. The sign of the bias was, however, expected to be reversed as the illusion was applied to the reference line contrary to Experiment I where it was applied to the replica. Regarding saccades, if the previously reported effects can be entirely attributed to the CoG, no difference in bias should be

observed between the angles pointing in the same direction. On the contrary, if the illusion affects saccades beyond the CoG effect at least one significant difference among angles pointing in the same direction should be observed. Moreover, if the strength of the illusion is similar to the one observed on perceptual judgments, no significant interaction between Angle and Task should be observed in the interaction model.

We then explored the relationship between the illusion effect in the reproduction and the saccade tasks by performing a cross-participants Spearman rank-order correlation analysis on the individual slopes of the angle effect in each task.

4.2. Results

4.2.1. Length Reproduction Task

As in Experiment I, the LMM on the bias in the length reproduction task showed a significant main effect of Angle, $F(6, 2824.3) = 272.10$, $p < .001$, $\eta^2p = .37$, $BF_{10} = 3.04 \times 10^{152}$, indicating a progressive shift from –13.50 % (SE = 0.55 %) to +7.12% (SE = 0.71 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values < .01; see detailed statistics in Supplementary Table 2 of Appendix A), except between angles +45° and +67.5°, $t(2828) = 1.08$, $p = 1.000$ (Figure 4A).

4.2.2. Saccade Task

The LMM on the bias in the saccade task showed a significant main effect of Angle, $F(6,2678.2) = 172.16$, $p < .001$, $\eta^2p = .28$, $BF_{10} = 7.00 \times 10^{152}$, indicating a progressive shift from –20.27 % (SE = 0.83 %) to +2.78% (SE = 0.77 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant

differences between all pairs (all *p*-values < .001; see detailed statistics in Supplementary Table 2 of Appendix A), except between angles -67.5° and -45°, $t(2678) = -2.24$, $p = .149$, and between angles -45° and -22.5°, $t(2678) = -1.53$, $p = .754$ (Figure 4B).

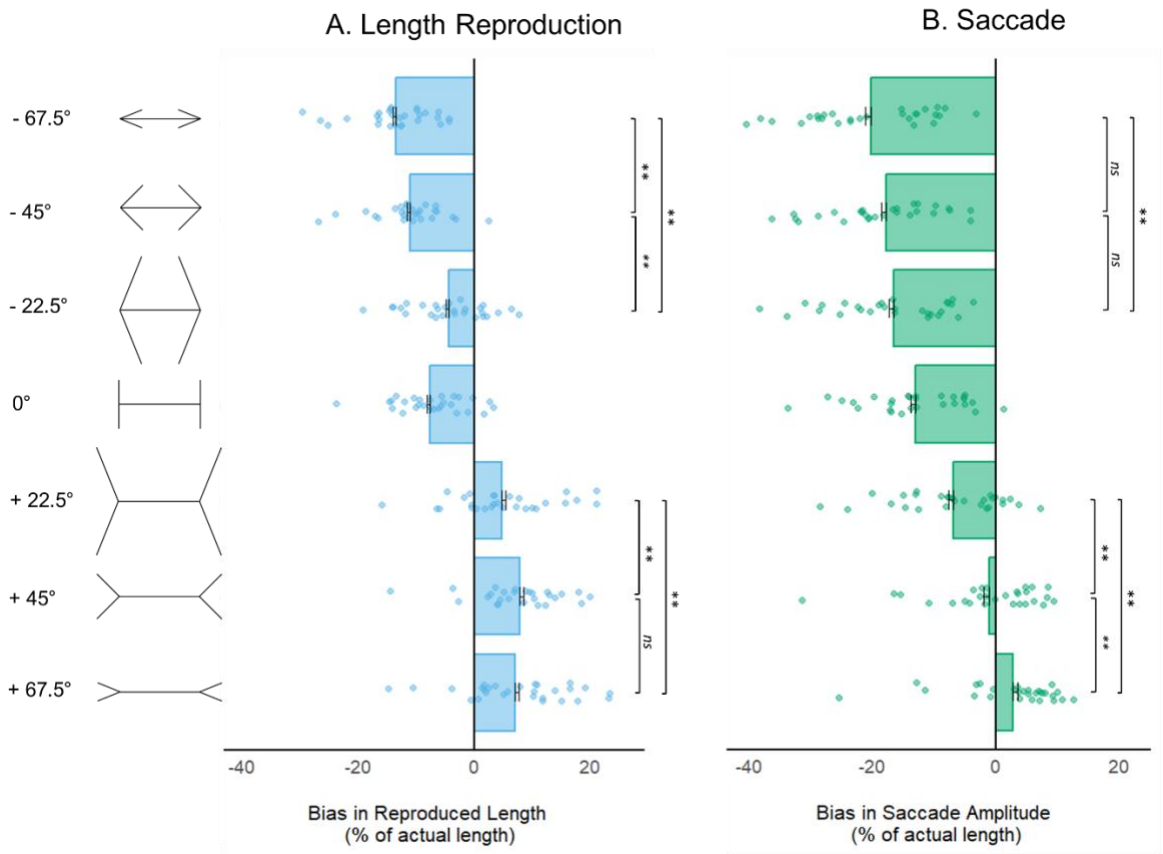


Figure 4. The bias in the [A] reproduced length and [B] saccade amplitude induced by the constant-projection variant of the Müller-Lyer illusion of Experiment II (expressed in percentage of the actual length of the horizontal segment). Error bars represent the S.E. and dots represent the individual means. Note that while individual means are plotted, statistical analyses were conducted on single-trial data (using mixed-effects modeling).
** *p*-value < .01; *ns p-value > 0.05*

4.2.3. Illusion Strength as a function of Task

The LMM including the interaction between Angle and Task showed a significant main effect of Angle, $F(1, 5539.4) = 1911.59$, $p < .001$, $\eta^2p = .26$, $BF_{10} = \infty$. The sign of the slope of the angle's effect ($\beta = 0.17$, $p < .001$) was consistent with the increase found in the separate analyses. There was also a significant effect of Task, $F(1,5540.6) = 489.54$, $p < .001$, $\eta^2p =$

.08, BF_{10} = 5.67 × 10^{75}, indicating greater underestimation in saccade amplitude (M = –10.24 %, SE = 0.34 %) than in the reproduced length (M = -2.42 %, SE =0.28%). Importantly, there was no significant Angle by Task interaction, $F(1,5540.1) = 0.96$, $p = .326$, $\eta^2p < .01$, $BF_{10} < 0.001$, providing strong evidence that the effect of angle, and thus illusion, was similar across tasks.

The correlation analysis showed a positive correlation between the slope of the effect of angle in the reproduction task and the slope of the effect in the saccade task, $\rho = .32$, $p = .046$, suggesting that participants who exhibited a stronger illusion effect in the reproduction task also tended to show a stronger effect in the saccade task.

V. Experiment III

Experiment II showed that saccadic eye movements were modulated by angle's amplitude. Overall, saccade amplitude tended to be smaller than the length of the horizontal segment. This underestimation was the strongest for the wings-in configurations with the sharpest angles and progressively decreased as the angle amplitude increased. The observed effects were comparable to those observed in the length reproduction task. Importantly, significant differences in bias were observed across angles sharing the same CoG, indicating that the illusion's effect on saccadic (and perceptual) behavior cannot be explained solely by CoG differences. However, it remains possible that variability in how the CoG is computed contributes to these effects. The CoG account supposes that each arrow is perceived as a triangle whose outline is partly illusory since the only visible sides are the fins. The saliency of the illusory side may diminish or take longer to emerge in configurations with shallower angles, where the fin tips are more widely spaced, leading to a reduced influence

of the CoG for those angles. Indeed, it has been shown that the saliency of the CoG depends on the specific spatial arrangement of the constituent elements (e.g., Gegenfurtner et al., 1997; Vishwanath & Kowler, 2003) and on their effective visibility (Vishwanath et al., 2000). To address this potential confound, Experiment III required participants to perform saccades on MLI configuration in which the triangles formed by the fins were explicitly filled in, turning the illusory contour into a physically defined one.

5.1. Methods

5.1.1. Participants

Twenty-six different Caucasian students (22 females and 4 males, M_{age} = 20 years, SD_{age} = 2 years) from the Université catholique de Louvain, Belgium, participated in this study during April 2025. Participant eligibility, sample size determination, and ethical procedures were identical to those described in Experiment I.

5.1.2. Apparatus and Stimuli

The same apparatus and stimuli as in Experiment II were used.

5.1.3. Procedure

Participants performed the same saccade task as in Experiment II, with one key modification: the surface area of the triangle formed by the arrow fins was filled in with a uniform grey color (Figure 5). This change transformed the illusory contour connecting the two tips of the arrow's wing from Experiment I and II into an explicit visual boundary. Participants completed the same training phase and number of trials as for the saccade task of Experiment II.

5.1.4. Data Analyses

Eye data were extracted and pre-processed as in Experiment II. 2.20 % of the trials were excluded because no saccade covering more than half of the horizontal segment was detected during the trial; 4.39 % because a saccade of over half the horizontal segment occurred before the GO signal and 9.51 % because saccade amplitude and/or latency exceeded 3 times the individual's MAD for the concerned horizontal segment length (Leys et al., 2013). After these exclusions, the average saccade amplitude was 4.28° of visual angle (SE = 0.02°) and the average saccade latency was 331 msec (SE = 1 msec). The bias in saccade amplitude was then computed as in Experiment II.

We then fitted a LMM with Angle (7 levels: -67.5°, -45°, -22.5°, 0°, +22.5°, +45°, +67.5°) as a categorical fixed effect and Participant as a random intercept, along with the corresponding Bayesian analysis. The same planned pairwise contrasts as in Experiments I and II were used to compare angles pointing in the same direction (*i.e.*, with the same CoG). If the differences observed in Experiment II were due to greater difficulty in interpolating the illusory contour of the triangle evoked by shallower angles, then the saccade bias should no longer differ between angles with the same CoG in this new version of the task where the triangular shape was made explicit. Alternatively, the finding of significant differences between same-direction angles after making the triangular shape equally salient would provide additional evidence that the saccade bias is not due to CoG computations but to distortions of the represented length of the horizontal segment caused by the MLI.

5.2. Results

As in Experiment II, the LMM on the bias in saccade amplitude showed a significant main effect of Angle, $F(6, 2411.7) = 111.79$, $p < .001$, $\eta^2p = .22$, $BF_{10} = 3.79 \times 10^{94}$, indicating a progressive shift from −12.39 % (SE = 0.78 %) to 7.40 % (SE = 0.71 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values < .05; see detailed statistics in Supplementary Table 3 of Appendix A), except between angles -67.5° and -45°, $t(2411) = -1.12$, $p = 1.000$, and between angles -45° and -22.5°, $t(2411) = -1.66$, $p = 0.577$ (Figure 5).

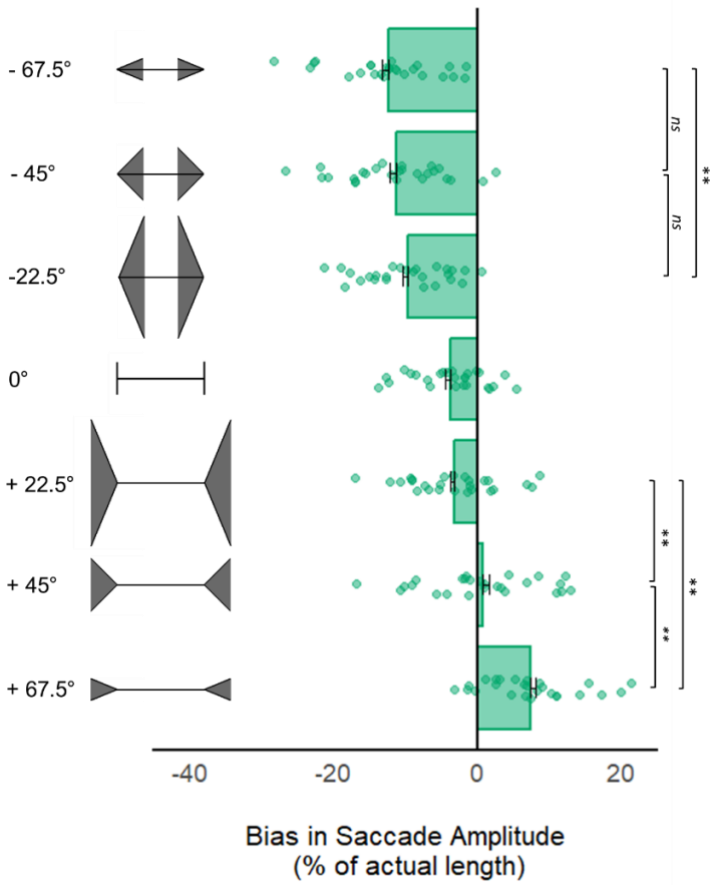


Figure 5. The bias in saccade amplitude performed along the horizontal segment of the constant-projection MLI figures of Experiment III (expressed in percentage of the actual length of the horizontal segment). Error bars represent the S.E. and dots represent the individual means. Note that while individual means are plotted, statistical analyses were conducted on single-trial data (using mixed-effects modeling).

** *p*-value < .01; *ns p-value > 0.05*

VI. Experiment IV

Experiment III replicated the effect of angle amplitude on saccadic eye movements, even when the connection between the fin tips was explicitly depicted. This finding rules out the possibility that the observed differences are due to greater difficulty computing the CoG of the triangle formed by the arrow when the fins are more spread apart. In this final experiment, we investigated whether the illusion effect on saccades intensifies with shorter previewing times as predicted by the hypothesis that perception and action share a visual representation that becomes more accurate over time. To do so, participants were asked to perform saccades along the horizontal segment of constant-projection MLI figures after either 50 or 2,000 ms of preview time.

6.1. Methods

6.1.1. Participants

Twenty-nine different Caucasian students (12 females and 17 males; M_{age} = 28 years; SD_{age} = 7 years) from the Université catholique de Louvain, Belgium, participated in this study between May and Augustus 2024. Participant eligibility and ethical procedures were identical to those described in Experiment 1. To determine the required sample size, we first replicated the G*Power estimation used in Experiment I for the individual analyses. Additionally, we conducted simulation-based power analyses using the simr package in R, following the procedure outlined by Green and MacLeod (2015), to estimate the number of participants needed to detect a small interaction effect between angle and preview. We began by deriving the regression coefficient corresponding to an interaction effect size of η^2_p = .02. This was achieved by proportionally scaling the squared regression coefficients based

on the angle effect observed on saccade in Experiment II (β = 0.17, η^2_p = .26), resulting in an estimated interaction coefficient of β = 0.04. Simulations indicated that a sample size of 8 participants would yield 80% power to detect this interaction using our design and analysis approach. Our final sample of 29 participants therefore provides ample power—achieving 100%—to detect the hypothesized interaction between angle and preview.

6.1.2. Apparatus and Stimuli

The same apparatus and stimuli as in Experiment II were used with one exception: the length of the horizontal segment of the MLI figure could be 4, 5, 6 or 7° of visual angle to induce more variability in the response as the timing of the GO signal was held constant within block (see below).

6.1.3. Procedure

The same saccade task as in Experiment II was used, with the key difference being that the red dot disappeared either after 2,000 ms (i.e., as in Experiment II) or 50 ms. The MLI configuration was thus previewed either for a short or long duration before participants initiated the saccade. The configuration remained visible from its appearance until the end of the saccade movement. The different preview conditions were presented in separate blocks. Before each preview condition, participants performed the same training phase as described in Experiment II. After this training, participants completed two blocks of the specific preview condition, with each block consisting of the seven possible angles repeated eight times—once for each combination of horizontal segment length and direction. The order of the preview conditions was counterbalanced across participants.

6.1.4. Data Analyses

Eye data were extracted and pre-processed as in Experiment II and III. 3.36 % of the trials were excluded because no saccade covering more than half of the horizontal segment was detected during the trial; 2.09 % because a saccade of over half the horizontal segment occurred before the GO signal and 3.90 % because saccade amplitude and/or latency exceeded 3 times the individual's MAD for the concerned horizontal segment length and angle amplitude (Leys et al., 2013). After these exclusions, the average saccade amplitude was 5.07° of visual angle (SE = 0.02°) for the short preview condition and 5.22° of visual angle (SE = 0.02) for the long preview condition. The average saccade latency was 245 msec (SE = 1 msec) in the short preview condition and 323 msec (SE = 1 msec) in the long preview condition. The bias in saccade amplitude was then computed as in previous experiments.

We conducted the same analyses as in Experiment II, except that Task was replaced by Preview (2 levels: 50 vs. 2,000 msec). The results of Experiment II and III predict significant differences between angles pointing to the same directions in the long preview condition (2,000 msec). If the illusion strength is negatively correlated to previewing time as previous studies suggested, these differences should be stronger in the short preview condition (50 msec), hence the interaction model should reveal a significant Angle by Preview interaction. Importantly, to show that the effect of time on illusion strength is not reducible to a CoG effect vanishing over time, it is essential to cancel out the CoG. This was done by expressing the bias for each angle as the absolute difference from the bias observed in the neutral configuration and then pooling angles across the wings-in and wings-out configurations. We then conducted an additional LMM and its Bayesian equivalent with Angle (coded as a

continuous variable in absolute terms relative to 0°), Preview (categorical, 2 levels: 50 ms vs. 2,000 ms), and their interaction as fixed effects, and Participant as a random intercept. A difference in the effect of absolute angle between the two preview conditions would provide evidence against a CoG account of the decreasing effect of illusion over time.

6.2. Results

6.2.1. Short Preview

The LMM on the bias in the short preview condition showed a significant main effect of Angle, $F(6, 3060.1) = 405.24$, $p < .001$, $\eta^2p = .44$, $BF_{10} = \infty$, indicating a progressive shift from –22.44% (SE = 0.66 %) to 7.54% (SE = 0.72 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values < .02; see detailed statistics in Supplementary Table 4 of Appendix A; Figure 6A).

6.2.2. Long Preview

As in Experiment II, the LMM on the bias in the long previewing condition showed a significant main effect of Angle, $F(6, 2785.4) = 127.68$, $p < .001$, $\eta^2p = .22$, $BF_{10} = 8.16 \times 10^{103}$, indicating a progressive shift from –13.53% (SE = 0.68 %) to 5.39% (SE = 0.71 %) between angles -67.5° and +67.5°. Pairwise *t*-tests between angles pointing in the same direction showed significant differences between all pairs (all *p*-values <.05; see detailed statistics in Supplementary Table 4 of Appendix A), except between angles -67.5° and -22.5° for which the difference was marginal, $t(2785) = -2.57$, $p = .061$, and between angles -45° and -22.5°, for which there was no significant difference, $t(2785) = 0.73$, $p = 1.000$ (Figure 6B).

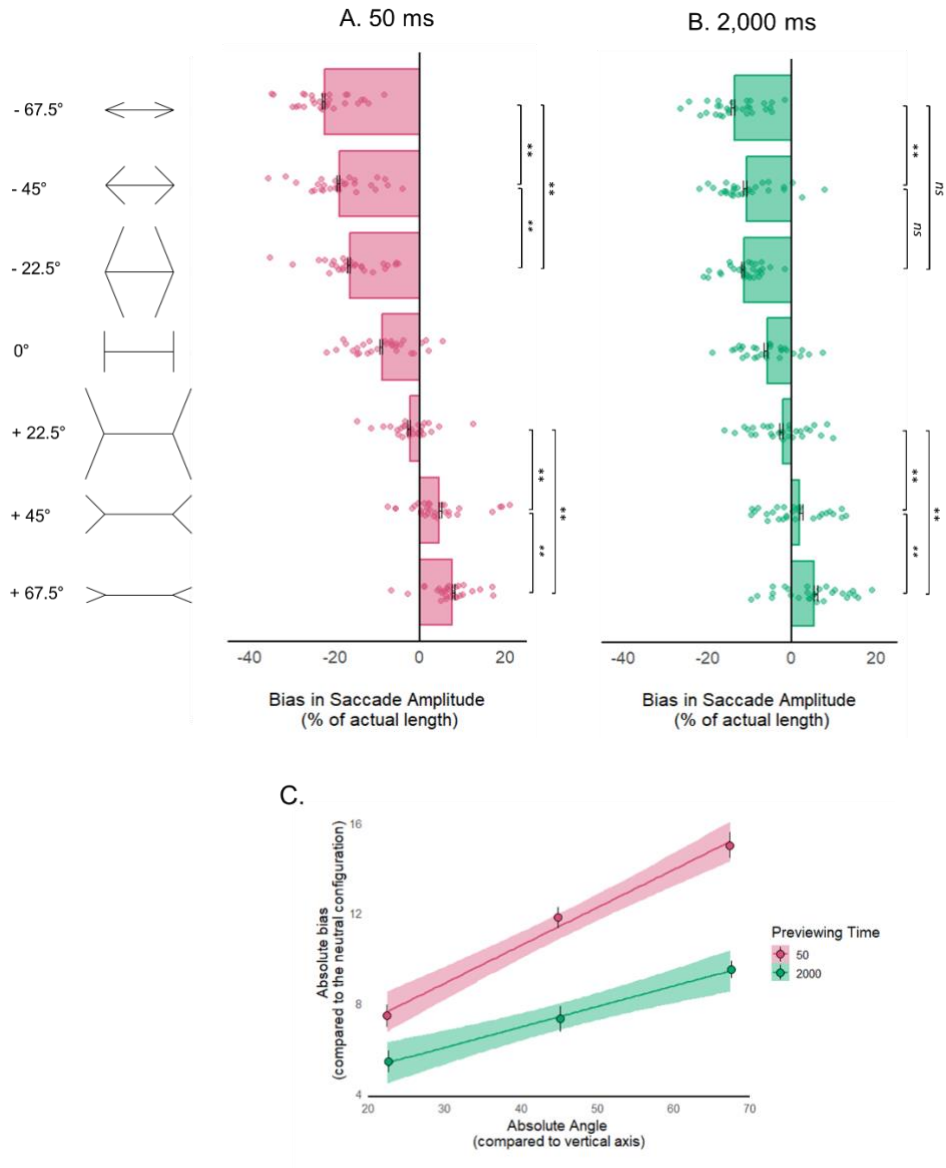


Figure 6. [A] The bias in saccade amplitude in the short (50 ms) and **[B]** long (2,000 ms) previewing time conditions of Experiment IV (expressed in percentage of the actual length of the horizontal segment). Error bars represent the SE and dots represent the individual means. Note that while individual means are plotted, statistical analyses were conducted on single-trial data (using mixed-effects modeling). **[C]** Effect of absolute angle (relative to the vertical axis) on absolute saccadic bias (relative to the neutral configuration) as a function of previewing time in Experiment IV. Colored dots indicate group means, with vertical error bars representing the SE. Shaded areas around the regression lines denote the SE of the model fit.

** *p*-value < .01; *ns p-value > 0.05.*

6.2.3. Illusion Strength as a function of Preview

The LMM including the interaction between Angle and Task showed a significant main effect of Angle, $F(1, 5883.1) = 2{,}676.54$, $p < .001$, $\eta^2p = .31$, $BF_{10} = \infty$. There was also a

significant effect of Preview, $F(1, 5886.7) = 69.57$, $p < .001$, $\eta^2p = .01$, $BF_{10} = 2.74 \times 10^9$, indicating greater underestimation in the short preview condition (M ± SE = –7.99 ± 0.31° of visual angle) than in the long preview condition (-5.15 ± 0.29° of visual angle). Importantly, there was also a significant Angle by Preview interaction, $F(1, 5883.3) = 170.33$, $p < .001$, $\eta^2p = .03$, $BF_{10} = 5.65 \times 10^{34}$, indicating that the effect of angle, and thus illusion, was less strong for the long previewing time ($\beta = 0.14$, $p = .001$) than for the short previewing time ($\beta = 0.24$, $p = .001$).

The LMM on the absolute bias showed a main effect of Absolute Angle, $F(1, 142) = 178.76$, $p < .001$, $\eta^2p = .56$, $BF_{10} = 1.01 \times 10^{14}$, indicating that the absolute bias increased as the angle deviated from the vertical axis (or neutral configuration). There was also a significant interaction with Preview, $F(1,142) = 15.50$, $p < .001$, $\eta^2p = .11$, $BF_{10} = 78.85$, indicating that the effect of the absolute angle was less strong for the long previewing time ($\beta = 0.09$, $p = .001$) than for the short previewing time ($\beta = 0.17$, $p = .001$; Figure 6).

VII. Discussion

The goal of this study was to evaluate two competing hypotheses regarding the influence of visual illusions on oculomotor behavior. According to the two visual streams hypothesis (Goodale & Milner, 1992; Milner & Goodale, 2006, 2008), saccadic eye movements are resistant to visual illusions because they rely on visual processes that represent object metrics independently of the visual context. In contrast, an alternative hypothesis proposes that saccades are influenced by visual illusions, similar to perceptual judgments, as both rely on a visual representation that is influenced by contextual information (e.g., Franz, 2001) but becomes more accurate with increased processing time

(van Zoest & Hunt, 2011). Critical evidence comes from studies showing that saccades performed across a horizontal segment are shorter when the segment is flanked by wings-in arrows, which make the segment appear shorter, and longer when flanked by wings-out arrows, which make it appear longer (Bruno et al., 2010; MacKeith & Knox, 2012). Besides, this effect has been shown to be substantiated under short previewing times (De Grave & Bruno, 2010; de Brouwer et al., 2014; Medendorp et al., 2018; van Zoest & Hunt, 2011). However, a key limitation of these findings is that they can be attributed to the CoG of the arrows attracting the saccade endpoint independently of a misrepresentation of the segment's length (Coren & Hoenig, 1972; Findlay, 1982; He & Kowler, 1989), an effect that also amplifies under previewing times (Coeffe & O'Regan, 1987). To address this limitation, we systematically manipulated the amplitude of the angles formed by the fins of the arrows while adjusting their lengths to ensure that the CoG remained constant across angles pointing in the same direction, allowing us to disentangle illusion and CoG effect. The results showed that (1) the perceived length of the horizontal segment progressively increased with angle amplitude even across angle pointing in the same direction, (2) the amplitude of saccades made along the horizontal segment were biased by angle amplitude to the same extent as perceptual judgements, (3) the bias in saccades could not be attributed to a greater difficulty in computing the CoG of the triangle formed by the arrow when the fins are more spread apart and (4) the bias in saccades was less pronounced with a long previewing time (2,000 msec) than with a long previewing time (50 msec). In contrast with previous studies, these data provide non-ambiguous evidence for an effect of the MLI because the saccadic error was not the mere difference between wings-in (<->) and wings-out (>-<) configurations but a linear function of angle amplitude also observed across angle pointing in the same

direction. We observed this parametric modulation after equating the horizontal projection of the fins within each type of configuration. Such an experimental manipulation allowed us to conclude that the amplitude of saccadic eye movements changed with the perceived length and not with the CoG, which remained constant within a particular configuration. It also contributed to clarifying that the decreasing effect of illusion with longer previewing time was not due to the CoG effect vanishing over time. It could have been argued, indeed, that saccades are more strongly biased towards the CoG when the imperative signal comes shortly after the stimulus onset, leaving less time for accurate oculomotor programming. However, we showed that the effect of time on illusion strength was maintained when angle amplitudes were converted to absolute values, thus eliminating CoG differences between the wings-in and wings-out configurations. We also ruled out the possibility that reduced fixation accuracy, particularly gaze shifts, during the long preview condition, account for differences observed relative to the short preview condition, by showing that gaze did not deviate significantly beyond 0.5° of visual angle from the fixation point and did not differ from the short preview condition (see Methods and detailed results in Appendix B).

Despite extensive investigation, there remains no consensus regarding the mechanism underlying the MLI. Researchers who suggest that its influence on saccadic eye movements stems from a CoG motor effect that is independent from perceptual length distortion (e.g., de Grave et al., 2006; Chen et al., 2020; Gilster & Kuhtz-Buschbeck, 2010) implicitly rely on CoG-independent accounts to explain the perceptual effect (e.g., the misapplied size constancy, which posits that arrowheads act as depth cues, leading the brain to misjudge line length; Gregory, 1968). However, not all interpretations of the MLI exclude a role for CoG mechanisms. Some efference-based accounts posit that, upon viewing the MLI

figure, a potential eye movement biased toward the CoG is computed and retained, which in turn biases length perception toward that CoG (Virsu, 1971; Coren, 1986; Delucia et al., 1994). Yet, prior evidence has shown that perceptual distortion can be disrupted even when a CoG effect persists (Chen et al., 2020; Gilster & Kuhtz-Buschbeck, 2010). Our findings corroborate and extend this dissociation: the illusion endures at both motor and perceptual levels when CoG is held constant, challenging the sufficiency of efference-based accounts. Others proposed that the visual system struggles to isolate the shaft endpoints from the arrowheads, resulting in a mislocalization of the segment's endpoints toward the CoG of the flanking arrowheads, resulting, in turn, in a misrepresentation of the segment's length (Morgan et al., 1990; Searleman et al., 2005). Again, this account fails to account for the perceptual bias we observed across configurations that share the same CoG. Later, Bulatov and colleagues (2009; 2010) refined the definition of CoG, arguing that the visual system cannot compute an exact physical CoG of the lightness distribution of the endpoint and attached flankers. Instead, it would rely on a "physiological" centroid of local luminance distribution, which would be modulated by the attentional window's profile. This physiological centroid is sensitive to variations in angle amplitude, even when horizontal projections are held constant (Bulatov et al., 2022). Thus, we cannot rule out that CoG-related mechanisms, albeit not in the physical sense, contribute to the effects observed in our data. At the same time, our results remain compatible with other theoretical accounts, such as the already mentioned misapplied size constancy theory (Gregory, 1968) or the confusion theory, which posits that perceived length is influenced by the distance between arrowhead tips (Erlebacher & Sekuler, 1971; Sekuler & Erlebacher, 1969; Woodworth, 1938). The present results contradict theories assuming that *only* the saccade bias observed in the

context of Müller-Lyer illusion would be due to CoG computation, whereas the perceptual bias induced by this illusion would be due to another mechanism independent of the CoG. The question of which common mechanism could account for the effect of MLI on saccade and perceptual biases remains open, especially if one considers that they may coexist (Woloszyn, 2010; Phillips, 2016). Bulatov and colleagues' proposal implies a distortion of the encoded length that is independent of motor programming, and can thus explain both perceptual and saccadic biases, like the misapplied size constancy theory (Gregory, 1963) or the confusion theory (Erlebacher & Sekuler, 1971; Sekuler & Erlebacher, 1969; Woodworth, 1938). Crucially for our research question, the finding that length judgments and saccades are affected similarly by angle or previewing time provide strong evidence for the hypothesis that perception and oculomotor behavior rely on a shared visual representation that is influenced by visual context but becomes more precise with increased processing time.

The perceptual nature and the time course of the reported effects make it difficult to maintain that saccadic eye movements rely on distinct processes that protect them against the length distortions induced by the visual context. The finding that ballistic eye movements are influenced by the illusory content of the display questions the hypothesis that perception and action used different metrics (Goodale & Milner, 1992; Milner & Goodale, 2006). It could be argued that saccades are influenced by context-induced illusions because object processing in the ventral stream has sufficient time to interfere with saccade programming in the dorsal stream. The ventral and dorsal streams would work independently to compute object metrics in allocentric and egocentric coordinates, respectively, but a cross-over would be possible over time (e.g., Goodale, 2011). According to this view, illusion effects should increase with previewing time. The results of Experiment III do not verify this prediction,

showing that illusion effects are in fact greater when the saccade is immediate than when it occurs after a long previewing time. These findings challenge the notion of independent processing streams for perception and action, instead supporting the view that both rely on an integrated visual representation influenced by context, with a dynamic interplay that diminishes rather than amplifies illusory effects over time. The idea of a shared representation between perception and action was further supported by the observation that participants who exhibited a stronger perceptual illusion effect in the reproduction task also tended to show a stronger modulation in the saccade task.

The notion of a shared representation between visual perception and saccades aligns with a growing body of research in spatial localization and motor planning, suggesting that the perceptual and oculomotor systems are not entirely independent but rely on common spatial coding mechanisms. Specifically, evidence from saccadic adaptation paradigms have shown that systematic changes in saccade amplitude lead to corresponding shifts in perceptual localization, suggesting that perceptual and oculomotor space are encoded within a shared coordinate system (Zimmermann & Lappe, 2016). The effect of perceptual requirements on subsequent saccade amplitude and direction further supports the idea of bidirectional interactions between the perceptual and oculomotor systems (Schütz et al., 2014). The present study extends these interactions to length representation by demonstrating that saccade amplitudes are biased by the visual context in a manner consistent with its effect on perceptual length judgments. The idea of a shared representation of length influenced by contextual cues is also supported by neuroimaging studies linking contextual illusions to structural and functional aspects of the primary visual cortex (V1), which is known to send projections to both the ventral and dorsal streams. For instance, V1

activity (Murray et al., 2006), surface area (Schwarzkopf et al., 2011), and central visual cortical magnification (Schwarzkopf et al., 2013) have been shown to correlate with the perceived size of illusory stimuli. This suggests that V1 contributes to a general, context-sensitive representation of object size that feeds into both the ventral and dorsal streams.

The increasing accuracy of length representation over time may reflect the growing influence of top-down processes during visual processing. Indeed, top-down control has been shown to increase with saccade latency (Ghahghaei & Verghese, 2015; Ludwig & Gilchrist, 2002; Salinas et al., 2019; Schütz et al., 2012; van Zoest et al., 2004), likely because extended processing time allows the system to resolve early, stimulus-driven biases (Wolf & Lappe, 2020). This resonates with broader theories of visual processing, particularly those emphasizing the interplay between feedforward and feedback mechanisms. Early in visual processing, feedforward pathways rapidly propagate sensory information from the retina through the lateral geniculate nucleus (LGN) to V1, creating a coarse representation of the visual scene. As processing time increases, feedback mechanisms from higher-order areas, such as the parietal and prefrontal cortices, provide iterative refinement of the initial representation. These feedback loops are thought to enable more precise computations (Lamme & Roelfsema, 2000). This dynamic interaction might thus underlie the time-dependent reduction of the illusion effect (see de Brouwer et al., 2014 for a similar discussion). Future studies could investigate the neural mechanisms underlying this refinement, using neuroimaging or electrophysiological methods to explore the temporal dynamics of context influence in greater detail. Understanding these temporal dynamics not only enriches theoretical models of visual processing but also has practical implications. For instance, investigating how feedback mechanisms compensate for distorted or ambiguous

visual input could inform rehabilitation strategies for individuals with impairments in saccadic control or perceptual integration, such as those following stroke or traumatic brain injury.

The results also raise compelling points concerning the added value of using different metrics to support perception and saccade programming. If perception and action were to operate with entirely distinct metrics, how would effective communication and coordination between these systems be achieved? A shared metric system addresses this challenge by offering a seamless interface for integrating perceptual information and translating it into motor commands. Such a unified framework would facilitate rapid and efficient interactions between perception and action, enabling coherent and adaptive behavior. Moreover, is it truly advantageous for action to disregard visual context when computing an object's metrics? Visual context provides critical information about distance. Indeed, to estimate distance, the brain integrates binocular cues, such as the disparity between images from each eye, with monocular cues derived from visual context, including relative size, brightness, position, linear perspective foreshortening, and texture gradients (Gibson, 1950; Howard & Rogers, 2002; Surdick et al., 1994). Distance is not only critical *per se* for action but also for determining an object's size, a factor equally crucial for motor tasks. The retinal size of an object depends not only on its real size but also on its distance from the observer. Thus, the motor system must compute relative metrics, at least of the different scene elements, to accurately infer an object's distance and size. This perspective provides insight into why actions are influenced by the arrowheads of the MLI, which are assumed to be interpreted as depth cues (McGraw & Stanford, 1994). For instance, when the arrow points inward, the configuration is often perceived as sloping away, akin to the corner of a building. This depth cue suggests the line is farther away and therefore shorter. Conversely, an outward-pointing

configuration resembles the corner of a room sloping toward the observer, creating the impression that the line is closer and thus longer. The brain adjusts the perceived length based on the most probable distance inferred from these cues. While this mechanism is adaptive and usually accurate, it can lead to miscalibrations in cases like the MLI. Thus, the susceptibility of action to visual context, such as in the MLI, underscores the importance of a shared metric system that incorporates visual context to enhance the precision of motor responses in natural environments.

VIII. Constraints on generality

Although the sample was restricted to healthy Caucasian young adults with normal or corrected-to-normal vision, there is little reason to expect that the core principles demonstrated here—such as the influence of visual context on perceptual and oculomotor representations—would not hold more broadly. Indeed, the general structure and organization of the visual system are largely consistent across humans, with very few systematic differences across genders, ethnicities or other demographic variables, making our results largely generalizable despite the homogeneity of our samples.

The findings of this study are based on saccadic eye movements performed in response to the Müller-Lyer illusion under controlled laboratory conditions. While this raises questions about whether the results generalize to more complex visual environment, the Müller-Lyer illusion represents a well-documented case of context-induced distortions in both perception and action. Its use is therefore a valid model for investigating the influence of visual context on oculomotor behavior. Future studies should extent these results to more complex and naturalistic environments.

Finally, the results of the present study are constrained to saccadic eye movements and generalizing them to other types of motor actions, such as reaching or grasping, should be approached with caution. Nonetheless, saccades engage the dorsal visual stream, suggesting that this stream is less immune to visual context effects than assumed by the two-visual-stream theory (Goodale & Milner, 1992; Milner & Goodale, 2006, 2008). More prototypical motor responses such as grasping movements have been reported to show partial immunity to visual illusions than perceptual judgements (Aglioti et al. 1995; Haffenden & Goodale, 1998). Such discrepancies may be due to online corrections during movement execution. In support of this, some evidence suggests that illusion effects on grip aperture are more pronounced during the early, ballistic phase of grasping and diminish during the later phases that engage on-line control based on visual feedback (Glover & Dixon, 2001; 2002). Although those results have been debated due to methodological concerns (e.g., Franz et al., 2005), a recent study by Uccelli & Bruno (2024) replicated the decrease in illusion effects over time while addressing previous limitations. Interestingly, they showed that this decrease only occurs when visual feedback is available, thus enabling effective online corrections. This pattern suggests that action-related size representations are initially susceptible to contextual effects but are refined as the movement unfolds, likely due to corrections mediated by visual feedback. However, the debate about the vulnerability of grasping movements to visual illusions remains open as other studies using different methodologies found discrepant results (Westwood et al., 2001; Franz et al., 2005). This emphasizes the need to consider evidence from studies testing other actions or modalities that provide better control on online correction. For instance, the mental imagery of an impending grasp—where no online correction can occur—proved to be affected by context-

induced illusions (Geers et al., 2019; 2021). Similarly, saccadic eye movements offer limited opportunities for correction once initiated and are consistently affected by visual illusions. Taken together with previous findings on related actions, the present results thus suggest that while visual context does influence action, this effect can be mitigated by compensatory mechanisms during movement execution or by allowing extended processing time before movement onset. Finally, the evidence for a time-dependent refinement of visual representations aligns with broader principles of sensory-motor integration, indicating that similar mechanisms might apply across a range of tasks involving perception and action.

IX. Conclusion

In conclusion, our findings provide compelling evidence that perceptual judgments and saccadic eye movements are guided by a common visual representation influenced by visual context. The time-dependent refinement of this representation underscores the dynamic nature of visual processing. These results not only challenge the strict dichotomy proposed by the two visual streams hypothesis but also offer a more integrated perspective on the interplay between perception and action within the visual system.

X. References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current biology*, *5*(6), 679-685.

Bernardis, P., Knox, P., & Bruno, N. (2005). How does action resist visual illusion? Uncorrected oculomotor information does not account for accurate pointing in peripersonal space. *Experimental Brain Research*, *162*, 133-144.

Binsted, G., & Elliott, D. (1999). The Müller–Lyer illusion as a perturbation to the saccadic system. *Human Movement Science*, *18*(1), 103-117.

Bruno, N., Knox, P. C., & de Grave, D. D. (2010). A metanalysis of the effect of the Müller-Lyer illusion on saccadic eye movements: no general support for a dissociation of perception and oculomotor action. *Vision Research*, *50*(24), 2671-2682.

Bulatov, A., Bertulis, A., Bulatova, N., & Loginovich, Y. (2009). Centroid extraction and illusions of extent with different contextual flanks. *Acta Neurobiologiae Experimentalis*, *69*(4), 504-525.

Bulatov, A., Bertulis, A., Gutauskas, A., Mickiene, L., & Kadziene, G. (2010). Center-of-mass alterations and visual illusion of extent. *Biological Cybernetics*, *102*, 475-487.

Bulatov, A., Bulatova, N., Marma, V., & Kučinskas, L. (2022). Quantitative study of asymmetry in the manifestation of the wings-in and wings-out versions of the Müller-Lyer illusion. *Attention, Perception, & Psychophysics*, *84*(2), 560-575.

Bürkner P (2017). “brms: An R Package for Bayesian Multilevel Models Using Stan.” *Journal of Statistical Software*, *80*(1), 1–28.

Chen, J., Yang, P., & Chen, Z. (2020). The effect of the Müller–Lyer configuration on saccadic eye movements is not fully due to illusory perception. *Journal of Neurophysiology*, *124*(3), 856-867.

Coëffé, C., & O'regan, J. K. (1987). Reducing the influence of non-target stimuli on saccade accuracy: Predictability and latency effects. *Vision research*, *27*(2), 227-240.

Coren, S., & Hoenig, P. (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and motor skills*, *34*(2), 499-508.

Christie, P. S. (1975). Asymmetry in the Müller-Lyer illusion: Artifact or genuine effect?. *Perception*, *4*(4), 453-457.

de Brouwer, A. J., Brenner, E., Medendorp, W. P., & Smeets, J. B. (2014). Time course of the effect of the Müller-Lyer illusion on saccades and perceptual judgments. *Journal of vision*, *14*(1), 4-4.

de Grave, D. D., & Bruno, N. (2010). The effect of the Müller-Lyer illusion on saccades is modulated by spatial predictability and saccadic latency. *Experimental Brain Research*, *203*, 671-679.

de Grave, D. D., Smeets, J. B., & Brenner, E. (2006). Why are saccades influenced by the Brentano illusion?. *Experimental Brain Research*, *175*, 177-182.

de Haan, E. H., Jackson, S. R., & Schenk, T. (2018). Where are we now with 'What'and 'How'?. *Cortex*, *98*, 1-7.

Delucia, P. R., Longmire, S. P., & Kennish, J. (1994). Diamond-winged variants of the Müller-Lyer figure: a test of Virsu's (1971) centroid theory. *Perception & psychophysics*, *55*(3), 287-295.

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in psychology*, *5*, 781.

Earlebacher, A., & Sekuler, R. (1969). Explanation of the Muller-Lyer illusion: Confusion theory examined. *Journal of Experimental Psychology*, *80*(3p1), 462.

Festinger, L., White, C. W., & Allyn, M. R. (1968). Eye movements and decrement in the Müller-Lyer illusion. *Perception & psychophysics*, *3*, 376-382.

Findlay, J. M. (1982). Global visual processing for saccadic eye movements. *Vision research*, *22*(8), 1033-1045.

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in cognitive sciences*, *5*(11), 457-459.

Franz, V. H., Scharnowski, F., & Gegenfurtner, K. R. (2005). Illusion effects on grasping are temporally constant not dynamic. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(6), 1359.

Geers, L., Pesenti, M., & Andres, M. (2018). Visual illusions modify object size estimates for prospective action judgements. *Neuropsychologia*, *117*, 211-221.

Geers, L., Pesenti, M., Derosiere, G., Duque, J., Dricot, L., & Andres, M. (2021). Role of the fronto-parietal cortex in prospective action judgments. *Scientific Reports*, *11*(1), 7454.

Geers, L., Vannuscorps, G., Pesenti, M., & Andres, M. (2022). Selective interference of hand posture with grasping capability estimation. *Experimental brain research*, 1-11.

Gegenfurtner, K. R., Brown, J. E., & Rieger, J. (1997). Interpolation processes in the perception of real and illusory contours. *Perception*, *26*(11), 1445-1458.

Ghahghaei, S., & Verghese, P. (2015). Efficient saccade planning requires time and clear choices. *Vision research*, *113*, 125-136.

Gibson, J. J. (1950). The perception of visual surfaces. *The American journal of psychology*, *63*(3), 367-384.

Gilster, R., & Kuhtz-Buschbeck, J. P. (2010). The Müller-Lyer illusion: Investigation of a center of gravity effect on the amplitudes of saccades. *Journal of Vision*, *10*(1), 11-11.

Glover, S. R., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. Journal of Experimental Psychology: Human Perception and Performance, 27(3), 560.

Glover, S., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. *Perception & Psychophysics*, *64*, 266-278.

Goodale, M. A. (2011). Transforming vision into action. *Vision research*, *51*(13), 1567-1587.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences*, *15*(1), 20-25.

Green, P., & MacLeod, C. J. (2016). SIMR: An R package for power analysis of generalized linear mixed models by simulation. *Methods in Ecology and Evolution*, *7*(4), 493-498.

Gregory, R. L. (1968). Visual illusions. Scientific American, 219(5), 66–76.

Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of cognitive Neuroscience*, *10*(1), 122-136.

Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth, Vol. 2: Depth perception*. University of Toronto Press.

Jeffreys, H. (1998). *The theory of probability*. OuP Oxford.

Knox, P. C., & Bruno, N. (2007). When does action resist visual illusion? The effect of Müller–Lyer stimuli on reflexive and voluntary saccades. *Experimental Brain Research*, *181*, 277-287.

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in neurosciences*, *23*(11), 571-579.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2019). Package "Emmeans". R Package Version 4.0-3.

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of experimental social psychology*, *49*(4), 764-766.

Ludwig, C. J., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: human perception and performance*, *28*(4), 902.

Mackeith, D. C., & Knox, P. C. (2012). Saccades and the Müller-Lyer illusion: implications for the two-visual-systems hypothesis. *British and Irish Orthoptic Journal*, *9*, 23-29.

McGraw, K. O., & Stanford, J. (1994). The apparent distance of interior and exterior corners: a test of Gregory's misapplied size constancy explanation for the Mueller-Lyer illusion. *The Journal of general psychology*, *121*(1), 19-26.

Medendorp, W. P., de Brouwer, A. J., & Smeets, J. B. (2018). Dynamic representations of visual space for perception and action. *Cortex*, *98*, 194-202.

Milner, D., & Goodale, M. (2006). *The visual brain in action* (Vol. 27). Oup Oxford.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774-785.

Morgan, M. J., Hole, G. J., & Glennerster, A. (1990). Biases and sensitivities in geometrical illusions. *Vision research*, *30*(11), 1793-1810.

Munoz, D. P. (2002). Commentary: saccadic eye movements: overview of neural circuitry. *Progress in brain research*, *140*, 89-96.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature neuroscience*, *9*(3), 429-434.

Open Science Collaboration. (2015). Estimating the reproducibility of psychological science. Science, 349(6251): aac4716.

Phillips, I. (2016). Naïve realism and the science of (some) illusions. *Philosophical Topics*, *44*(2), 353-380.

Piaget, J. (2013). *The mechanisms of perception*. Routledge.

Rossetti, Y., Pisella, L., & McIntosh, R. D. (2017). Rise and fall of the two visual systems theory. *Annals of physical and rehabilitation medicine*, *60*(3), 130-140.

Salinas, E., Steinberg, B. R., Sussman, L. A., Fry, S. M., Hauser, C. K., Anderson, D. D., & Stanford, T. R. (2019). Voluntary and involuntary contributions to perceptually guided saccadic choices resolved with millisecond precision. *ELife*, *8*, 1–22.

Schenk, T., & Hesse, C. (2018). Do we have distinct systems for immediate and delayed actions? A selective review on the role of visual memory in action. *Cortex*, *98*, 228-248.

Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. *Journal of vision*, *14*(5), 4-4.

Schütz, A. C., Trommershäuser, J., & Gegenfurtner, K. R. (2012). Dynamic integration of information about salience and value for saccadic eye movements. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(19), 7547–7552.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature neuroscience*, *14*(1), 28-30.

Schwarzkopf, D. S., & Rees, G. (2013). Subjective size perception depends on central visual cortical magnification in human V1. *PloS one*, *8*(3), e60550.

Searleman, A., Porac, C., Dafoe, C., & Hetzel, B. (2005). Altering Mueller-Lyer illusion magnitude using figural additions at the wing-shaft intersections. *The American journal of psychology*, *118*(4), 619-637.

Sekuler, R., & Erlebacher, A. (1971). The two illusions of Müller-Lyer: Confusion theory reexamined. *The American Journal of Psychology*, 477-486.

Surdick, R. T., Davis, E. T., King, R. A., Corso, G. M., Shapiro, A., Hodges, L., & Elliot, K. (1994). Relevant cues for the visual perception of depth: is where you see it where it is?. *Proceedings of the Human Factors and Ergonomics Society Annual Meeting*, *38* (19), 1305-130.

Uccelli, S., & Bruno, N. (2024). The effect of the Uznadze illusion is temporally dynamic in closed-loop but temporally constant in open-loop grasping. *Quarterly Journal of Experimental Psychology*, *77*(6), 1238-1249.

van Zoest, W., Donk, M., & Theeuwes, J. (2004). The role of stimulus-driven and goal-driven control in saccadic visual selection. *Journal of Experimental Psychology: Human Perception and Performance*, *30*(4), 746–759.

van Zoest, W., & Hunt, A. R. (2011). Saccadic eye movements and perceptual judgments reveal a shared visual representation that is increasingly accurate over time. *Vision Research*, *51*(1), 111-119.

Virsu, V. (1971). Tendencies to eye movement, and misperception of curvature, direction, and length. *Perception & Psychophysics*, *9*, 65-72.

Vishwanath, D., & Kowler, E. (2003). Localization of shapes: Eye movements and perception compared. *Vision Research*, *43*(15), 1637-1653.

Vishwanath, D., Kowler, E., & Feldman, J. (2000). Saccadic localization of occluded targets. *Vision Research*, *40*(20), 2797-2811.

Weidner, R., & Fink, G. R. (2007). The neural mechanisms underlying the Müller-Lyer illusion and its interaction with visuospatial judgments. *Cerebral Cortex*, *17*(4), 878-884.

Westwood, D. A., McEachern, T., & Roy, E. A. (2001). Delayed grasping of a Müller-Lyer figure. *Experimental brain research*, *141*, 166-173.

Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real-time control of action. *Spatial vision*, *16*(3-4), 243-254.

Wolf, C., & Lappe, M. (2020). Top-down control of saccades requires inhibition of suddenly appearing stimuli. *Attention, Perception, & Psychophysics*, *82*, 3863-3877.

Woloszyn, M. R. (2010). Contrasting three popular explanations for the Muller-Lyer illusion. *Current Research in Psychology*, *1*(2), 102-107.

Woodworth, R. S., & Schlosberg, H. (1954). *Experimental psychology*. Oxford and IBH Publishing.

Yarbus, A. L., & Yarbus, A. L. (1967). Eye movements during perception of complex objects. *Eye movements and vision*, 171-211.

Zimmermann, E., & Lappe, M. (2016). Visual space constructed by saccade motor maps. *Frontiers in Human Neuroscience*, *10*, 225.