

## Full Length Article

## Simple actions modulate context-dependent visual size perception at late processing stages

Haoyang Yu<sup>a,b</sup>, Irene Sperandio<sup>c</sup>, Lihong Chen<sup>a,b,\*</sup><sup>a</sup> Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian 116029, China<sup>b</sup> Key Laboratory of Brain and Cognitive Neuroscience, Liaoning Province, Dalian 116029, China<sup>c</sup> Department of Psychology and Cognitive Science, University of Trento, Rovereto 38068, Italy

## ARTICLE INFO

Original content: [Simple actions modulate context-dependent visual size perception at late processing stages \(Original data\)](#)

## Keywords:

Simple action  
Perceived size  
Ebbinghaus illusion  
rTMS  
Interocular transfer

## ABSTRACT

A simple button press towards a prime stimulus enhances subsequent visual search for objects that match the prime. The present study investigated whether this action effect is a general phenomenon across different task domains, and the underlying neural mechanisms. The action effect was measured in an unsped size-matching task, with the presentation of the central target and the surrounding inducers of the Ebbinghaus illusion together to one eye or separately to each eye, and when repetitive TMS was applied over right primary motor cortex (M1). The results showed that a prior key-press significantly reduced the illusion effect compared to passive viewing. Notably, the action effect persisted with dichoptic presentation of the Ebbinghaus configuration, but disappeared with the right M1 disruption. These results suggest that action guides visual perception to influence human behavior, which mainly affects the late visual processing stage and probably relies on feedback projections from the motor cortex.

## 1. Introduction

It is well-established that action is tightly linked to visual perception. The way in which individuals interact with an object can determine which object features are preferentially processed by the visual system. For example, it has been shown that an individual's ability to judge stimulus size is enhanced during the planning phase of a grasping movement, compared to a pointing movement (Wykowska, Schubö, & Hommel, 2009). Additionally, studies have shown that when planning a whole hand power grasp, selective attention is biased towards larger objects, whereas planning a pinch precision grasp facilitates attention detection of smaller objects (Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008). In other words, action planning biases selective attention towards congruent action-related features. There is also evidence that the perceived size of an object is heavily underestimated after grasping, compared to reaching, and this size underestimation is unaffected by tactile feedback (Bosco, Daniele, & Fattori, 2017; Sanz Diez, Bosco, Fattori, & Wahl, 2022). Taken together, these findings support the notion that preparing for a certain type of action facilitates the processing of stimulus features that are relevant for the control of the planned action.

Recently, it has been suggested that not only goal-directed actions (i.

e., grasping or pointing), but also simple arbitrary actions towards an object, such as a key press, are able to influence subsequent visual perception and attention of the acted-on object in a following task unrelated to the action. This phenomenon has been referred to as the *action effect* (Han, Ji, Choe, Kim, & Kim, 2020; Wang, Sun, Sun, Weidler, & Abrams, 2017; Wang, Weidler, Sun, & Abrams, 2021; Weidler & Abrams, 2014, 2016). In the original paradigm developed by Buttaccio and Hahn (Buttaccio & Hahn, 2011), participants were required to either press a key in response to or merely view a colored circle (i.e., the prime), and then immediately perform a visual search task. Relative to passive viewing, a prior key-press facilitated target detection when the target appeared in the prime's color and impaired target detection when the distractor appeared in the prime's color (Buttaccio & Hahn, 2011). Other studies have shown that the action effect can still be observed even when the prime is rendered invisible by means of continuous flash suppression (Suh & Abrams, 2018), and when the action is planned during the prime's presentation but executed only after completing a visual search task (Han et al., 2020). Numerous investigations have replicated and extended these findings by revealing that the features of a previously acted-on object are also prioritized in a pop-out search (Weidler & Abrams, 2016), and can bias eye movements during the search (Wang et al., 2017).

\* Corresponding author at: Research Center of Brain and Cognitive Neuroscience, Liaoning Normal University, Dalian 116029, China.

E-mail address: [lihongchen@lnnu.edu.cn](mailto:lihongchen@lnnu.edu.cn) (L. Chen).

It should be noted that previous research has primarily adopted speeded visual search task to explore the action effect on orientation discrimination. However, it remains unclear whether the action effect is a general phenomenon that can be extended to unspeeded visual tasks, and what neural underpinnings are responsible for this motor-induced modulation of visual perception. Here, we tested for the first time the effect of a prior button-press on the perceived size of an acted-on object by using the classic Ebbinghaus illusion in an unspeeded size-matching task. Given previous evidence that the action effect can be observed with a subliminal prime and across different response modalities (Suh & Abrams, 2018; Wang et al., 2017), it is plausible to assume that it might take effect at both early and late stages of visual processing. To probe this possibility, we used an interocular transfer paradigm, where the inner target circle and the surrounding elements of the Ebbinghaus illusion were presented either together to one eye only (i.e., monocular viewing condition) or separately to each eye (i.e., dichoptic viewing condition). Interocular transfer experiments elucidate how the visual inputs from each eye are processed along the geniculostriate pathway to determine if a phenomenon occurs at an early or late stage of visual processing (Schiller & Wiener, 1962; Song, Schwarzkopf, & Rees, 2011; Yildiz, Sperandio, Kettle, & Chouinard, 2021). It is well-known that binocular integration primarily occurs in the primary visual cortex (V1), and nearly all neurons beyond V1 are binocular (Hubel & Wiesel, 1968; Song et al., 2011; Zeki, 1978). Given this organization, we hypothesized that if the action effect influences late visual processing, then we would expect to observe this motor-based modulation during dichoptic viewing condition, as a result of interocular transfer. Conversely, if the action effect is solely manifested during monocular viewing condition, then we would infer that this phenomenon primarily affects early visual processing.

The human primary motor cortex (M1) plays an essential role in generating individual finger movements, such as pressing a button (Diedrichsen, Wiestler, & Krakauer, 2013; Ejaz, Hamada, & Diedrichsen, 2015; Yokoi, Arbuckle, & Diedrichsen, 2018). Previous studies using transcranial magnetic stimulation (TMS) have demonstrated that applying inhibitory theta bursts stimulation over the contralateral M1 disrupted implicit sequence learning of finger movements, which required participants to press four buttons with different fingers of the right hand in response to visual stimuli (Wilkinson, Teo, Obeso, Rothwell, & Jahanshahi, 2010). Similar results were observed when static magnetic stimulation was applied to the contralateral M1 (Lacroix et al., 2019). Furthermore, there is ERP evidence indicating that the amplitude of the readiness potential – a slow negative-going component recorded in fronto-parietal sites 1–2 s before the execution of a voluntary movement (Libet, Gleason, Wright, & Pearl, 1983) – can predict differences in discrimination accuracy of gratings presented around the onset of the action (Benedetto, Ho, & Morrone, 2022).

On the basis of these findings, we hypothesized that the action-based modulation on subsequent visual processing might be mediated by feedback projections originating in M1. To test this possibility, we temporarily disrupted M1 activity using inhibitory TMS before measuring the action effect. If M1 plays a causal role in this process, we would expect to find a significant reduction or elimination of the action effect following M1 disruption.

## 2. Methods

### 2.1. Participants

A total of forty-eight healthy participants (21 males; mean age  $\pm$  SD:  $22.1 \pm 2.1$  years old) took part in the study. The study consisted of three experiments. Each experiment involved 16 participants (Experiment 1: eight males, mean age  $\pm$  SD:  $22.9 \pm 1.9$  years old; Experiment 2: seven males, mean age  $\pm$  SD:  $21.5 \pm 2.6$  years old; Experiment 3: six males, mean age  $\pm$  SD:  $22.0 \pm 1.4$  years old). The sample size was determined using G\*Power software (Faul, Erdfelder, Lang, & Buchner, 2007) to

estimate the minimum sample size to reach 0.90 power for repeated-measures ANOVA with a mean effect size of 0.58 drawn from a previous similar study (Buttaccio & Hahn, 2011).

All participants were right-handed, had normal or corrected-to-normal vision, had no metallic implants, and reported no history of neurological or psychiatric illness. They received monetary compensation for their time. The study was approved by the institutional review board of Liaoning Normal University and was conducted in accordance with the tenets of the Declaration of Helsinki. Written informed consent was obtained from all participants prior to testing.

### 2.2. Apparatus

The experiments were programmed in MATLAB (MathWorks, Natick, MA) with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were presented on an LCD monitor (19-in. Lenovo L197WA) with a resolution of  $1920 \times 1080$  pixels and a refresh rate of 60Hz. Participants were seated in front of the computer monitor in a dimly lit room with their heads stabilized by a chin rest. The viewing distance was 57 cm.

### 2.3. Stimuli and procedures

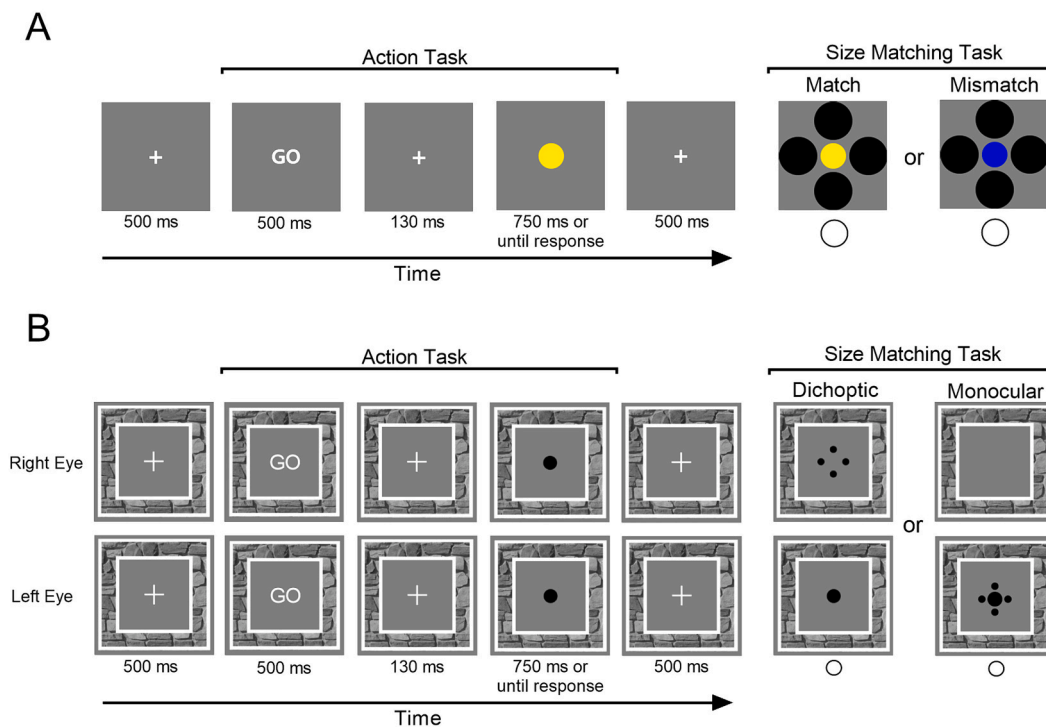
The Ebbinghaus configuration consisted of a central circle (diameter =  $1.1^\circ$ ; blue or yellow in Experiment 1, luminance = 39 and  $227 \text{ cd/m}^2$ , respectively; black in Experiments 2 and 3, luminance =  $0 \text{ cd/m}^2$ ) surrounded by four black circles, either large (diameter =  $1.7^\circ$ ; luminance =  $0 \text{ cd/m}^2$ ) or small (diameter =  $0.6^\circ$ ; luminance =  $0 \text{ cd/m}^2$ ). The Ebbinghaus illusion was displayed on a gray background (luminance =  $128 \text{ cd/m}^2$ ). The comparison stimulus for the size-matching task was a black circle (luminance =  $0 \text{ cd/m}^2$ ) positioned directly below the Ebbinghaus configuration ( $8.6^\circ$  from the screen center). The initial size of the comparison circle was randomly selected from  $0.8^\circ$  to  $1.4^\circ$  in  $0.06^\circ$  steps on each trial.

#### 2.3.1. Experiment 1: action effect on illusory size perception

The purpose of this experiment was to determine if prior action can modulate susceptibility to the Ebbinghaus illusion. In this experiment (Fig. 1A), participants were asked to complete an action task first, immediately followed by a size-matching task. At the beginning of each trial, a white fixation cross (size:  $1.5^\circ \times 1.5^\circ$ ) was presented at the center of the screen for 500 ms. Then, the word “GO” or “NO” in white font (size:  $2.3^\circ \times 1.3^\circ$ ) replaced the fixation cross for 500 ms (i.e., go/no-go task, see below). After that, the fixation cross reappeared for another 130 ms, followed by a prime stimulus. The prime could be either a yellow or blue circle (diameter =  $1.1^\circ$ ), which was presented at the screen center until the participant made the response or for a maximum of 750 ms in case of no response. Participants were instructed to perform a go/no-go task depending on the cue word they previously saw (i.e., ‘GO’ or ‘NO’). In the go trials, they had to react as quickly as possible by pressing the space bar upon the onset of the prime, using their left hand. In the no-go trials, they had to refrain from responding and passively view the prime. After the offset of the prime, the fixation cross was presented for 500 ms followed by the Ebbinghaus configuration displaying a yellow or blue target circle surrounded by four black circles, either large or small. Participants were required to perform a size-matching task, by adjusting the size of a black comparison circle until it matched that of the target circle. The task was performed with their right hand without time limit. There were 88 trials in total with 11 repetitions for each condition: size of inducers (large vs. small); prime-target color congruency (match vs. mismatch); action condition (key-press vs. passive viewing). The trials were presented randomly.

#### 2.3.2. Experiment 2: interocular transfer of the action effect

This experiment was carried out to determine if motor-induced changes in illusory perception involved early or late stages of visual



**Fig. 1.** Illustration of the experimental procedures. (A) In Experiment 1, the prime and the Ebbinghaus configuration were presented one after the other. Participants had to sequentially perform the action task and the size-matching task on each trial. For the action task, participants were asked to react as quickly as possible to the prime by pressing a button only when they previously saw the cue word 'GO'. For the size-matching task, participants were asked to adjust the size of the comparison circle to match that of the central target. (B) In Experiment 2, the cue words (i.e., 'GO' or 'NO') and the prime were always presented to both eyes, whereas the target circle and the surrounding inducers of the Ebbinghaus configuration were presented together to one eye (monocular viewing condition) or separately to each eye (dichoptic viewing condition).

processing. The experimental setting was identical to Experiment 1, with the following exceptions: i) the color of the prime and the target circle was set to black; ii) participants viewed the stimuli through a mirror stereoscope. The cue words "GO" and "NO", as well as the prime, were presented to both eyes.

The inner target circle and the surrounding inducers of the Ebbinghaus configuration were presented either together to one eye (left or right) in the monocular viewing condition or separately to each eye in the dichoptic viewing condition. Specifically, the left eye was presented with the target circle, while the surrounding inducers of the illusion were displayed to the right eye or vice versa under the dichoptic viewing condition. To aid binocular fusion, a textured frame was introduced around the illusory configuration (Fig. 1B). The frame was  $9.1^\circ$  by  $9.1^\circ$  with a thickness of  $1.7^\circ$ . As in Experiment 1, participants were required to sequentially perform both the action task and the size-matching task on each trial. There were 88 trials in total with 11 repetitions for each condition: size of inducers (large vs. small); viewing condition (monocular vs. dichoptic); action condition (key-press vs. passive viewing). The trials were presented randomly.

### 2.3.3. Experiment 3: probing the causal role of M1

The purpose of Experiment 3 was to establish the causal contribution of M1 to the effect of prior action on visual perception using repetitive TMS (rTMS). The stimuli and procedure were identical to those described in Experiment 1, except that the color of both the prime and the target circle was changed to black. At the beginning of the experiment, either real-rTMS or sham-rTMS was applied over the right M1. Immediately after the stimulation, participants completed both the action task and the size-matching task sequentially on each trial. Real and sham stimulation were tested in two separate blocks. The order of these two blocks was counterbalanced across participants, with a minimum interval of one week between them. There were 88 trials with 11

repetitions for each condition: size of inducers (large vs. small); stimulation condition (real vs. sham); action condition (key-press vs. passive viewing). Within each block, trials were presented in a random fashion.

### 2.4. TMS protocol

A PowerMAG stimulator (Mag & More, Berlin, Germany) with a figure of 8-shaped coil (Double coil PMD70-pCool) was used to deliver stimulation. One cortical site was chosen for stimulation: right M1. In accordance with previous studies (Lefaucheur et al., 2017; Mori et al., 2010), TMS was applied to the C4 site of the international 10–20 system to stimulate the right M1. The coil was held tangentially to the skull and was oriented such that the coil-center was overlaying the right M1. Participants received a 10-min 1-Hz train of pulses, which can produce inhibition of the stimulated cortical site (Hilgetag, Théoret, & Pascual-Leone, 2001; Mevorach, Humphreys, & Shalev, 2005, 2006) prior to the beginning of the experiment. Stimulation intensity was set at 90 % of the individual resting motor threshold, which was defined as the minimal strength of stimulation capable of inducing a reliable twitch in the left hand in at least 5 out of 10 trials with the right M1 stimulation (average threshold: 60 % of maximum stimulator output). The frequency, intensity, and duration of the stimulation were well within safe limits. The setup of sham stimulation was identical to that of real stimulation except using a sham coil, which produced the same clicking noise characterizing the delivery of an active TMS pulse but did not emit any effective stimulation to the targeted site. Participants were naive to the stimulation conditions.

### 2.5. Statistical analysis

Statistical analyses were performed using the JASP software (version 0.14.1, JASP Team). All reported  $p$  values are based on two-tailed

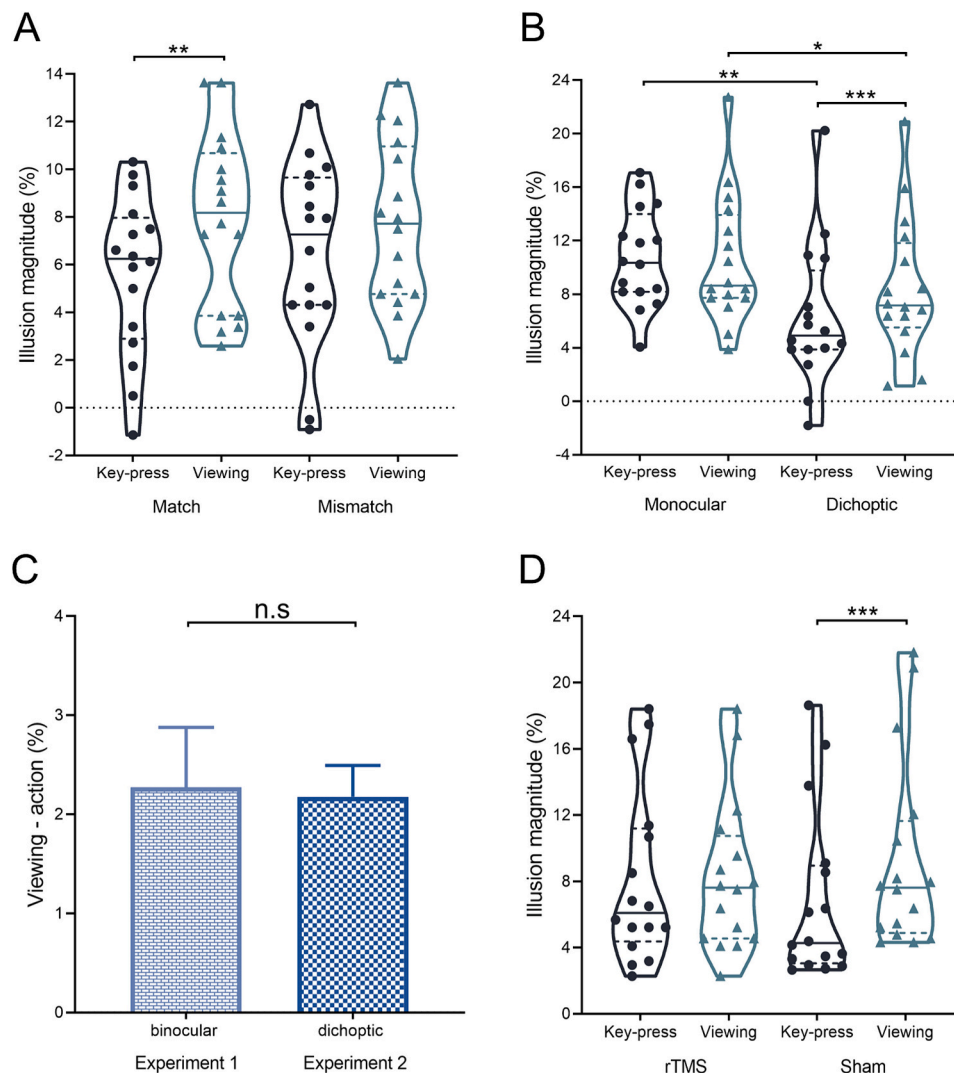
criteria. The mean accuracy and reaction time (RT) were calculated for each participant. Trials with incorrect response to the action task and with response times longer than 750 ms (i.e., delays) were removed from further analysis. The illusion magnitude was calculated as the difference of the perceived size of the central target surrounded by small and large circles relative to its physical size (%). All three experiments adopted a within-subject design. A  $2 \times 2$  repeated measures ANOVA was carried out on the illusion magnitude with Action condition (key-press vs. passive viewing) and Color congruency (match vs. mismatch) as main factors in Experiment 1. In Experiment 2, we performed a  $2 \times 2$  repeated measures ANOVA with Action condition (key-press vs. passive viewing) and Viewing condition (monocular vs. dichoptic) as main factors. Finally, in Experiment 3 we performed a  $2 \times 2$  repeated measures ANOVA with Action condition (key-press vs. passive viewing) and TMS stimulation (real vs. sham) as main factors. Partial eta squared ( $\eta_p^2$ ) was calculated to assess effect size. Post-hoc tests were Bonferroni-corrected for multiple comparisons and used to further examine any significant interaction.

### 3. Results

#### 3.1.1. Experiment 1: action effect on illusory size perception

Accuracy of the action task was measured as the percentage of correct responses to the primes (i.e., key-press for go-trials and passive viewing for no-go trials). The mean accuracy of the action task was 98.4% ( $SD = 1.8\%$ ) and the mean RT was 312 ms ( $SD = 5.8$ ; match condition:  $318 \pm 5.6$  ms; mismatch condition:  $306 \pm 6.3$  ms).

The perceptual effect of the illusion was 6.9% on average ( $SD = 3.6$ ). Results of the ANOVA revealed that the main effect of Action condition was significant ( $F(1,15) = 19.765, p < .001, \eta_p^2 = 0.569$ ). However, the main effect of Color congruency ( $F(1,15) = 1.201, p = .290, \eta_p^2 = 0.074$ ) and the Action condition  $\times$  Color congruency interaction ( $F(1,15) = 1.199, p = .291, \eta_p^2 = 0.074$ ) failed to reach significance. Further analysis showed that the illusion strength was significantly smaller for key-press than for passive viewing under match condition ( $t(15) = -3.708, p_{corr} = 0.005, d = 0.634$ ; Fig. 2 A), and this discrepancy was non-significant under mismatch condition ( $t(15) = -2.037, p_{corr} = 0.305, d = 0.348$ ).



**Fig. 2.** Experimental results. (A) The illusion magnitude as a function of action condition and color congruency in Experiment 1, and (B) as a function of action condition and viewing condition in Experiment 2. (C) Comparison of the action effect (passive viewing – key-press) between Experiment 1 with binocular presentation and Experiment 2 with dichoptic presentation. (D) The illusion magnitude as a function of action condition and TMS stimulation in Experiment 3. Error bars denote one standard error of the mean (SEM). Asterisks (\*) indicate significance levels of \*  $p < .05$ , \*\*  $p < .01$  and \*\*\*  $p \leq 0.001$ .

Therefore, these results demonstrate that when the Ebbinghaus illusion was preceded by a simple action (button-press) in response to a prime stimulus, the magnitude of the illusion was significantly reduced with respect to when a prior action was not required.

### 3.1.2. Experiment 2: interocular transfer of the action effect

The mean accuracy of the action task was 98.8 % ( $SD = 1.2$  %) and the mean RT was 312 ms ( $SD = 7.8$ ; monocular condition:  $315 \pm 8.2$  ms; dichoptic condition:  $309 \pm 7.5$  ms). The perceptual effect of the illusion was 9.0 % on average ( $SD = 5.0$ ). Results of the ANOVA showed that the main effects of both Action condition ( $F(1,15) = 6.749, p = .020, \eta_p^2 = 0.310$ ) and Viewing condition ( $F(1,15) = 12.522, p = .003, \eta_p^2 = 0.455$ ) were significant. Moreover, their interaction also reached significance,  $F(1,15) = 8.325, p = .011, \eta_p^2 = 0.357$ . Post-hoc comparisons with Bonferroni-correction showed that the illusion magnitude following a key-press was significantly smaller than that following passive viewing under dichoptic condition ( $t(15) = -3.882, p_{corr} = 0.003, d = 0.456$ ; Fig. 2B). In contrast, the comparison between key-press and passive viewing under monocular condition was not significant ( $t(15) = 0.325, p_{corr} = 1, d = 0.038$ ). Since the effect of prior action on the magnitude of the illusion emerged in the dichoptic viewing condition, we can infer that the action effect primarily took effect at relatively late stages of visual size processing.

In line with previous research (Song et al., 2011), the illusion magnitude was significant under both monocular and dichoptic presentations ( $ps < 0.001$ ), with the former being significantly greater than the latter for both key-press ( $t(15) = 3.953, p = .001, d = 0.988$ ) and passive viewing ( $t(15) = 2.372, p = .032, d = 0.593$ ) conditions, suggesting that the processing of the Ebbinghaus illusion involves both monocular and binocular neurons.

We further analyzed the data and compared the action effect of dichoptic presentation in Experiment 2 with that of binocular presentation in Experiment 1. This comparison was achieved by subtracting the illusion magnitude of the key-press condition from the passive viewing condition. The results revealed comparable action effect between these two viewing conditions ( $t(30) = 0.138, p = .891, d = 0.049$ ; Fig. 2C).

It is worth noting that if the action effect primarily affected the late processing of the Ebbinghaus illusion, it could also be observed under monocular condition, as monocular information also entered the late processing stage. However, we did not observe significant action effect with monocular presentation. As monocular condition consisted of both monocular and binocular processing, and dichoptic condition included only binocular processing. We subtracted dichoptic condition from monocular condition, to probe the action effect on the monocular component of the Ebbinghaus illusion, and observed the opposite pattern of results (key-press vs. passive viewing:  $t(15) = 2.885, p = .011, d = 0.721$ ). Thus, the non-significant action effect with monocular presentation could be due to that it had an opposite influence on the monocular component of the Ebbinghaus illusion, which deserves further exploration. Moreover, previous studies have found that monocular neurons in V1 and lateral genicular nucleus of macaque monkeys are significantly suppressed in response to binocular stimulation (Dougherty et al., 2021; Dougherty, Cox, Westerberg, & Maier, 2019). This binocular suppression could be responsible for the comparable action effect between dichoptic (Experiment 2) and binocular (Experiment 1) conditions.

### 3.1.3. Experiment 3: probing the causal role of M1

The mean accuracy of the action task was 98.5 % ( $SD = 2.1$  %) and the mean RT was 319 ms ( $SD = 10.4$ ; real stimulation:  $302 \pm 10.8$  ms; sham stimulation:  $336 \pm 9.9$  ms). There was no significant difference in terms of RT ( $t(15) = 1.197, p = .250, d = 0.299$ ) between real and sham stimulations. The perceptual effect of the illusion was 8.1 % on average ( $SD = 5.2$ ). Results of the ANOVA showed that the main effect of Action condition was significant ( $F(1,15) = 12.384, p = .003, \eta_p^2 = 0.452$ ). The

main effect of TMS stimulation failed to reach significance ( $F(1,15) = 0.009, p = .924, \eta_p^2 = 0.006$ ). Notably, the Action condition  $\times$  TMS stimulation interaction was significant ( $F(1,15) = 23.699, p < .001, \eta_p^2 = 0.612$ ). Post-hoc comparisons revealed that the strength of the illusion decreased significantly following a key-press action relative to the passive viewing condition under sham stimulation ( $t(15) = -5.658, p_{corr} < 0.001, d = 0.477$ ; Fig. 2D). In contrast, the difference in illusion magnitude between key-press and passive viewing was not significant under real stimulation ( $t(15) = -0.142, p_{corr} = 1, d = 0.012$ ). This result clearly indicates that the action effect requires M1 activity in order to occur.

## 4. Discussion

In the present study, we carried out three experiments to demonstrate for the first time if the effect of prior action can modulate context-dependent size perception (Experiment 1), and which neural mechanisms are responsible for this phenomenon (Experiments 2 and 3).

We showed that a prior key-press in response to a prime circle significantly reduced the strength of the Ebbinghaus illusion compared to passive viewing (Experiment 1). This action effect persisted even when the central target and surrounding inducers of the Ebbinghaus configuration were simultaneously presented to separate eyes, as a result of interocular transfer (Experiment 2). Importantly, it disappeared with the disruption of the right M1 by rTMS, demonstrating the causal role of the primary motor cortex in this motor-driven modulation of perceived size (Experiment 3).

The impact of action planning and execution on visual size perception has been extensively studied in the literature. For example, studies have shown that the perceived size of two-dimensional bars is heavily underestimated following a grasping action in comparison to a reaching action (Bosco et al., 2017; Sanz Diez et al., 2022). Additionally, research has demonstrated that planning a grasping movement enhances the ability to detect deviations in object size (Fagioli, Hommel, & Schubotz, 2007; Wykowska et al., 2009; Wykowska & Schubö, 2012) and improves memory for size (Heuer & Schubö, 2017). There is also evidence, although controversial, that successful actions may increase the apparent size of target objects. Specifically, softball players with higher hitting skills as well as skilled archers with greater shot accuracy tend to overestimate the size of their targets in contrast to players or archers with lower skill levels (Gray, 2013; Lee, Lee, Carello, & Turvey, 2012; Witt & Proffitt, 2005). By the same token, golfers who exhibit superior performance tend to overestimate the size of golf holes compared to those with lower playing abilities (Witt, Linkenauger, Bakdash, & Proffitt, 2008). More recently, it has been shown that object manipulability, an action-related information, can affect the magnitude of the Ebbinghaus illusion: highly manipulable objects, such as a basketball, tended to be more resistant to the contextual influences of the illusion than less manipulable objects., like a watermelon (Chen, Zhu, Feng, Zhang, & Jiang, 2022). Several studies using the Ebbinghaus illusion have shown that the visual control of goal-directed actions, such as grasping, can escape the effects of the illusion, even though the perceptual experience of the target disc's size typically succumbs to it (Aglioni, DeSouza, & Goodale, 1995; Haffenden & Goodale, 1998; Whitwell, Garach, Goodale, & Sperandio, 2023). This dissociation between perception and action has been considered as behavioral evidence in support of the influential two-visual-systems account put forth by Goodale and Milner (Goodale & Milner, 1992; Milner & Goodale, 1995). According to this account, visual information is processed in two distinct, yet interconnected, neural pathways stemming from V1: a ventral stream from occipital to temporal cortex responsible for object recognition and a dorsal stream from occipital to parietal cortex responsible for visually-guided actions. This division of labour may accommodate the different computational requirements inherent in perception and action.

Our results confirm and extend these findings by showing that an arbitrary button-press action, which did not require any specification of size-related parameters, could still influence subsequent size perception, predominantly manifesting its impact during the later stages of visual size processing. In sum, the visuo-motor system, which is activated by action planning and execution, action experience and knowledge, as well as action properties of objects, can dynamically modulate the incoming perceptual information, possibly by increasing the attentional weight of the acted-on object.

Attention has often been regarded as an emergent ability of linking sensory representations to actions. The premotor theory of attention postulates that the programming of movement causes attention to shift towards the intended destination of the movement (Rizzolatti, Riggio, Dascola, & Umiltá, 1987). For instance, the preparation of reaching movements leads to enhanced visual perception and larger N1 amplitude in correspondence to the movement's goal locations, as opposed to the locations that are movement-irrelevant (Baldauf & Deubel, 2008, 2009; Baldauf, Wolf, & Deubel, 2006). Also, planning an action directed towards an item stored in visual working memory can bias attention towards that item when it appears in a subsequent visual detection task, as evidenced by faster saccadic eye movements (Trentin, Slagter, & Olivers, 2023). Furthermore, it can improve performance for memory items that have been presented at the locations corresponding to the movement goal, likely facilitated by the allocation of spatial attention to the action's targets (Heuer, Crawford, & Schubö, 2017). Therefore, it is reasonable to believe that in the current study, a prior key-press response to the prime may have attracted spatial attention towards the prime's location, thereby allocating less attention to the surrounding context. This, in turn, likely resulted in the reduced illusory effects observed.

It remains to be determined where in the brain the top-down attentional signals originate during the action effect. One likely possibility is that the feedback projections are generated in the motor areas and target the early visual cortex. In fact, it has been shown that activity in the early visual cortex can be modulated by higher-order areas involved in action planning and execution through top-down projections (Gallivan, Chapman, Gale, Flanagan, & Culham, 2019; Monaco, Gallivan, Figley, Singhal, & Culham, 2017; Singhal, Monaco, Kaufman, & Culham, 2013). Research has also demonstrated that the neural representations of an acted-on target object in the early visual cortex are modulated by movement preparation (grasp vs. reach, align vs. open reach), potentially via top-down connections (Gallivan et al., 2019; Velji-Ibrahim, Crawford, Cattaneo, & Monaco, 2022). Interestingly, Benedetto and colleagues reported that a prior button-press action can affect the perceptual discrimination of spatial frequencies of gratings. They demonstrated that the discrimination performance oscillates at theta frequency, and both the V1 BOLD response to gratings and the functional connectivity between V1 and M1 oscillate at the same rhythm (Benedetto, Binda, Costagli, Tosetti, & Morrone, 2021). By using inhibitory rTMS, the present study showed that disrupting the right M1 abolished the influence of prior action on size perception. This provides causal evidence that the top-down signals responsible for the action effect originate in the motor cortex. Whether the action effect requires a direct input of the motor cortex to the visual cortex or involves other cortical or subcortical relays remains to be clarified.

It should be noted that the duration of the prime was always 750 ms for passive viewing, but it was less than 750 ms for key-press condition. To probe the potential confounding effect of different prime durations, we conducted another experiment, during which the prime duration of 750 ms was adopted for both conditions. The results revealed significant action effect (key-press vs. passive viewing:  $t(7) = -2.648$ ,  $p = .033$ ,  $d = 0.936$ ), suggesting that differences in prime duration were not likely to influence the results.

Taken together, our findings offer compelling evidence that prior actions can influence context-dependent visual size perception. This influence mainly takes place at the late stages of visual processing and

relies on feedback projections originating from the motor cortex.

#### 4.1. Limitations of the study

The present experimental design did not allow us to directly assess the link between M1 TMS and activity of the visual cortex. This step will be critical in future studies to elucidate the functional role of inter-regional oscillations between motor and visual cortex during visual perception.

#### CRedit authorship contribution statement

**Haoyang Yu:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Irene Sperandio:** Writing – review & editing. **Lihong Chen:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

#### Acknowledgements

We thank Yongxing Lu, Xue Han and Qingqing Luo for their help in data collection. This work was supported by grants from the National Natural Science Foundation of China (32171047), the Liaoning Revitalization Talents Program (XLYC2203131), and the Basic Scientific Research Business Expenses of Undergraduate Universities in Liaoning Province (LS2024Q005).

#### References

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, 5(6), 679–685. [https://doi.org/10.1016/S0960-9822\(95\)00133-3](https://doi.org/10.1016/S0960-9822(95)00133-3)
- Baldauf, D., & Deubel, H. (2008). Visual attention during the preparation of bimanual movements. *Vision Research*, 48(4), 549–563. <https://doi.org/10.1016/j.visres.2007.11.023>
- Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: An event-related potential study. *Journal of Cognitive Neuroscience*, 21(1), 18–29. <https://doi.org/10.1162/jocn.2008.21021>
- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, 46(26), 4355–4374. <https://doi.org/10.1016/j.visres.2006.08.021>
- Benedetto, A., Binda, P., Costagli, M., Tosetti, M., & Morrone, M. C. (2021). Predictive visuo-motor communication through neural oscillations. *Current Biology*, 31(15), 3401–3408.e4. <https://doi.org/10.1016/j.cub.2021.05.026>
- Benedetto, A., Ho, H. T., & Morrone, M. C. (2022). The readiness potential correlates with action-linked modulation of visual accuracy. *Eneuro*, 9(6). <https://doi.org/10.1523/ENEURO.0085-22.2022>
- Bosco, A., Daniele, F., & Fattori, P. (2017). Reaching and grasping actions and their context shape the perception of object size. *Journal of Vision*, 17(12), 10. <https://doi.org/10.1167/17.12.10>
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Buttaccio, D. R., & Hahn, S. (2011). The influence of action on visual search: Behavioral response toward stimuli modifies the selection process. *Attention, Perception, & Psychophysics*, 73(5), 1453–1466. <https://doi.org/10.3758/s13414-011-0121-y>
- Chen, L., Zhu, S., Feng, B., Zhang, X., & Jiang, Y. (2022). Altered effective connectivity between lateral occipital cortex and superior parietal lobule contributes to manipulability-related modulation of the Ebbinghaus illusion. *Cortex*, 147, 194–205. <https://doi.org/10.1016/j.cortex.2021.11.019>
- Diedrichsen, J., Wiestler, T., & Krakauer, J. W. (2013). Two distinct ipsilateral cortical representations for individuated finger movements. *Cerebral Cortex*, 23(6), 1362–1377. <https://doi.org/10.1093/cercor/bhs120>
- Dougherty, K., Carlson, B. M., Cox, M. A., Westberg, J. A., Zinke, W., Schmid, M. C., ... Maier, A. (2021). Binocular suppression in the macaque lateral geniculate nucleus

- reveals early competitive interactions between the eyes. *Eneuro*, 8(2). <https://doi.org/10.1523/ENEURO.0364-20.2020>
- Dougherty, K., Cox, M. A., Westerberg, J. A., & Maier, A. (2019). Binocular modulation of monocular V1 neurons. *Current Biology*, 29(3), 381–391.e4. <https://doi.org/10.1016/j.cub.2018.12.004>
- Ejaz, N., Hamada, M., & Diedrichsen, J. (2015). Hand use predicts the structure of representations in sensorimotor cortex. *Nature Neuroscience*, 18(7), 1034–1040. <https://doi.org/10.1038/nn.4038>
- Fagioli, S., Hommel, B., & Schubotz, R. I. (2007). Intentional control of attention: Action planning primes action-related stimulus dimensions. *Psychological Research*, 71(1), 22–29. <https://doi.org/10.1007/s00426-005-0033-3>
- 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. *Behavior Research Methods*, 39(2), 175–191. <https://doi.org/10.3758/bf03193146>
- Gallivan, J. P., Chapman, C. S., Gale, D. J., Flanagan, J. R., & Culham, J. C. (2019). Selective modulation of early visual cortical activity by movement intention. *Cerebral Cortex*, 29(11), 4662–4678. <https://doi.org/10.1093/cercor/bhy345>
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. [https://doi.org/10.1016/0166-2236\(92\)90344-8](https://doi.org/10.1016/0166-2236(92)90344-8)
- Gray, R. (2013). Being selective at the plate: Processing dependence between perceptual variables relates to hitting goals and performance. *Journal of Experimental Psychology: Human Perception and Performance*, 39(4), 1124–1142. <https://doi.org/10.1037/a0030729>
- Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, 10(1), 122–136. <https://doi.org/10.1162/08992998563824>
- Han, S., Ji, E., Choe, E., Kim, D., & Kim, M.-S. (2020). Simple action planning can affect attentional allocation in subsequent visual search. *Psychonomic Bulletin & Review*, 27(5), 1014–1024. <https://doi.org/10.3758/s13423-020-01758-z>
- Heuer, A., Crawford, J. D., & Schubö, A. (2017). Action relevance induces an attentional weighting of representations in visual working memory. *Memory & Cognition*, 45(3), 413–427. <https://doi.org/10.3758/s13421-016-0670-3>
- Heuer, A., & Schubö, A. (2017). Selective weighting of action-related feature dimensions in visual working memory. *Psychonomic Bulletin & Review*, 24(4), 1129–1134. <https://doi.org/10.3758/s13423-016-1209-0>
- Hilgetag, C. C., Théoret, H., & Pascual-Leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced ‘virtual lesions’ of human parietal cortex. *Nature Neuroscience*, 4(9), 953–957. <https://doi.org/10.1038/nn0901-953>
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology*, 195(1), 215–243. <https://doi.org/10.1113/jphysiol.1968.sp008455>
- Lacroix, A., Proulx-Bégin, L., Hamel, R., De Beaumont, L., Bernier, P.-M., & Lepage, J.-F. (2019). Static magnetic stimulation of the primary motor cortex impairs online but not offline motor sequence learning. *Scientific Reports*, 9(1), 9886. <https://doi.org/10.1038/s41598-019-46379-2>
- Lee, Y., Lee, S., Carello, C., & Turvey, M. T. (2012). An archer’s perceived form scales the “hitableness” of archery targets. *Journal of Experimental Psychology: Human Perception and Performance*, 38(5), 1125–1131. <https://doi.org/10.1037/a0029036>
- Lefaucheur, J.-P., Antal, A., Ayache, S. S., Benninger, D. H., Brunelin, J., Cogiamanian, F., ... Paulus, W. (2017). Evidence-based guidelines on the therapeutic use of transcranial direct current stimulation (tDCS). *Clinical Neurophysiology*, 128(1), 56–92. <https://doi.org/10.1016/j.clinph.2016.10.087>
- Libet, B., Gleason, C. A., Wright, E. W., & Pearl, D. K. (1983). Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain*, 106(3), 623–642. <https://doi.org/10.1093/brain/106.3.623>
- Mevorach, C., Humphreys, G. W., & Shalev, L. (2005). Attending to local form while ignoring global aspects depends on handedness: Evidence from TMS. *Nature Neuroscience*, 8(3), 276–277. <https://doi.org/10.1038/nn1400>
- Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience*, 9(6), 740–742. <https://doi.org/10.1038/nn1709>
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Monaco, S., Gallivan, J. P., Figley, T. D., Singhal, A., & Culham, J. C. (2017). Recruitment of foveal retinotopic cortex during haptic exploration of shapes and actions in the dark. *The Journal of Neuroscience*, 37(48), 11572–11591. <https://doi.org/10.1523/JNEUROSCI.2428-16.2017>
- Mori, F., Codecà, C., Kusayanagi, H., Monteleone, F., Buttari, F., Fiore, S., Bernardi, G., Koch, G., & Centonze, D. (2010). Effects of anodal transcranial direct current stimulation on chronic neuropathic pain in patients with multiple sclerosis. *The Journal of Pain*, 11(5), 436–442. <https://doi.org/10.1016/j.jpain.2009.08.011>
- Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Multisensory Research*, 10(4), 437–442. <https://doi.org/10.1163/156856897x00366>
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1), 31–40. [https://doi.org/10.1016/0028-3932\(87\)90041-8](https://doi.org/10.1016/0028-3932(87)90041-8)
- Sanz Diez, P., Bosco, A., Fattori, P., & Wahl, S. (2022). Horizontal target size perturbations during grasping movements are described by subsequent size perception and saccade amplitude. *PLoS One*, 17(3), Article e0264560. <https://doi.org/10.1371/journal.pone.0264560>
- Schiller, P., & Wiener, M. (1962). Binocular and stereoscopic viewing of geometric illusions. *Perceptual and Motor Skills*, 15(3), 739–747. <https://doi.org/10.2466/pms.1962.15.3.739>
- Singhal, A., Monaco, S., Kaufman, L. D., & Culham, J. C. (2013). Human fMRI reveals that delayed action re-recruits visual perception. *PLoS One*, 8(9), Article e73629. <https://doi.org/10.1371/journal.pone.0073629>
- Song, C., Schwarzkopf, D. S., & Rees, G. (2011). Interocular induction of illusory size perception. *BMC Neuroscience*, 12(1), 27. <https://doi.org/10.1186/1471-2202-12-27>
- Suh, J., & Abrams, R. A. (2018). Action influences unconscious visual processing. *Attention, Perception, & Psychophysics*, 80(6), 1599–1608. <https://doi.org/10.3758/s13414-018-1509-8>
- Symes, E., Tucker, M., Ellis, R., Vainio, L., & Ottoboni, G. (2008). Grasp preparation improves change detection for congruent objects. *Journal of Experimental Psychology: Human Perception and Performance*, 34(4), 854–871. <https://doi.org/10.1037/0096-1523.34.4.854>
- Trentin, C., Slagter, H. A., & Olivers, C. N. L. (2023). Visual working memory representations bias attention more when they are the target of an action plan. *Cognition*, 230, Article 105274. <https://doi.org/10.1016/j.cognition.2022.105274>
- Velji-Ibrahim, J., Crawford, J. D., Cattaneo, L., & Monaco, S. (2022). Action planning modulates the representation of object features in human fronto-parietal and occipital cortex. *European Journal of Neuroscience*, 56(6), 4803–4818. <https://doi.org/10.1111/ejn.15776>
- Wang, F., Sun, J., Sun, P., Weidler, B. J., & Abrams, R. A. (2017). Influence of simple action on subsequent manual and ocular responses. *Attention, Perception, & Psychophysics*, 79(2), 389–395. <https://doi.org/10.3758/s13414-017-1280-2>
- Wang, Z., Weidler, B. J., Sun, P., & Abrams, R. A. (2021). Simple action alters attention towards visual features. *Attention, Perception, & Psychophysics*, 83(4), 1699–1712. <https://doi.org/10.3758/s13414-021-02259-4>
- Weidler, B. J., & Abrams, R. A. (2014). Decomposing the action effect: How simple actions affect subsequent perception. *Attention, Perception, & Psychophysics*, 76(4), 1242–1252. <https://doi.org/10.3758/s13414-014-0652-0>
- Weidler, B. J., & Abrams, R. A. (2016). Simple actions influence pop-out search. *Visual Cognition*, 24(7–8), 392–405. <https://doi.org/10.1080/13506285.2017.1289996>
- Whitwell, R. L., Garach, M. A., Goodale, M. A., & Sperandio, I. (2023). Looking at the Ebbinghaus illusion: Differences in neurocomputational requirements, not gaze-mediated attention, explain a classic perception-action dissociation. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 378(1869), Article 20210459. <https://doi.org/10.1098/rstb.2021.0459>
- Wilkinson, L., Teo, J. T., Obeso, I., Rothwell, J. C., & Jahanshahi, M. (2010). The contribution of primary motor cortex is essential for probabilistic implicit sequence learning: Evidence from theta burst magnetic stimulation. *Journal of Cognitive Neuroscience*, 22(3), 427–436. <https://doi.org/10.1162/jocn.2009.21208>
- Witt, J. K., Linkenauger, S. A., Bakdash, J. Z., & Proffitt, D. R. (2008). Putting to a bigger hole: Golf performance relates to perceived size. *Psychonomic Bulletin & Review*, 15(3), 581–585. <https://doi.org/10.3758/PBR.15.3.581>
- Witt, J. K., & Proffitt, D. R. (2005). See the ball, hit the ball. *Psychological Science*, 16, 937–938. <https://doi.org/10.1111/j.1467-9280.2005.01640.x>
- Wykowska, A., & Schubö, A. (2012). Action intentions modulate allocation of visual attention: Electrophysiological evidence. *Frontiers in Psychology*, 3(379), 1–15. <https://doi.org/10.3389/fpsyg.2012.00379>
- Wykowska, A., Schubö, A., & Hommel, B. (2009). How you move is what you see: Action planning biases selection in visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 35(6), 1755–1769. <https://doi.org/10.1037/a0016798>
- Yildiz, G. Y., Sperandio, I., Kettle, C., & Chouinard, P. A. (2021). Interocular transfer effects of linear perspective cues and texture gradients in the perceptual rescaling of size. *Vision Research*, 179, 19–33. <https://doi.org/10.1016/j.visres.2020.11.005>
- Yokoi, A., Arbuckle, S. A., & Diedrichsen, J. (2018). The role of human primary motor cortex in the production of skilled finger sequences. *The Journal of Neuroscience*, 38(6), 1430–1442. <https://doi.org/10.1523/JNEUROSCI.2798-17.2017>
- Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *The Journal of Physiology*, 277(1), 273–290. <https://doi.org/10.1113/jphysiol.1978.sp012272>