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The hand knows something that the eye does not: Reaching movements resist the Müller–Lyer illusion whether or not the target is foveated

Aidan A. Thompson [a], David A. Westwood [b,*]

[a] *School of Kinesiology and Health Science, York University, Toronto, Ontario, Canada*
[b] *School of Health and Human Performance, Dalhousie University, 6230 South Street, Halifax, Nova Scotia, Canada B3H 3J5*

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Abstract

Previous reports suggest that saccades are affected by the Müller–Lyer (ML) pictorial illusion, whereas reaching movements are not. It is unclear if the resistance of reaching to illusions depends on the concurrent engagement of the oculomotor system. Here we show that the endpoints and kinematics of reaching movements were unaffected by a peripherally viewed ML stimulus regardless of whether or not a concurrent saccade was carried out. Primary saccade endpoints were affected by the ML stimulus but secondary saccades were not. Perceptual judgments of target location were influenced by the ML stimulus in the expected direction. The resistance of reaching movements to pictorial illusions does not appear to depend on the concurrent engagement of the oculomotor system. Implications for models of oculomotor and upper limb control are discussed.

Keywords: Reaching; Saccade; Perception; Illusion; Action; Vision

Pictorial illusions often have little to no effect on the kinematics of target-directed actions, despite their robust effect on conscious perceptual experience [4]. Whereas a number of studies have reported that actions are affected by certain types of illusions, and that these effects can be more pronounced in the early versus later stages of the movement sequence [10], it is not clear that these reported effects are as great as one would predict based on the magnitude of the perceptual effects of the stimuli. The resistance of action to illusions is broadly consistent with Goodale and Milner's [12] proposal that perceptual and sensorimotor aspects of vision are mediated by distinct cortical pathways that transform sensory inputs in quite different ways. The sensorimotor transformations that take place in the dorsal visual stream are thought to use absolute metrics (which are context-independent), whereas the perceptual processes that take place in the ventral visual stream utilize relative metrics (which are context-dependent) [11].

Because the cortical substrates of the oculomotor and reaching control systems are both located within the dorsal stream [1], one might predict that movements of the eyes and hands would be equally resistant to pictorial illusions. Contrary to this prediction, a number of studies [2,3,9] report that saccadic eye movements are much more sensitive to pictorial illusions than reaching movements, even when the two movements are carried out concurrently. Binsted and Elliott [3] suggest that the resistance of reaching movements to illusions depends on visual and proprioceptive information derived from oculomotor fixation of the target stimulus; according to these authors, the reaching control system detects errors in saccadic programming and adjusts the arm movement accordingly. Consistent with this view, Gentilucci et al. [9] reported that reaching movements resisted the ML illusion when the target was viewed centrally but not when viewed peripherally; however, the location of the target in central versus peripheral vision was confounded with the location of the target relative to the body midline. Bernardis et al. [2] found that reaching movements (without concurrent eye movements) were unaffected by a peripherally viewed ML stimulus despite robust effects of the illusion on perceptual localization and saccadic eye movements. That study casts doubt on the notion that oculomotor engagement is necessary for reaching movements to resist the ML illusion, suggesting instead that the reaching and oculomotor systems simply utilize different mechanisms to transform peripheral vision of the target into motor commands.

Bernardis et al. did not compare reaching movements with and without concurrent eye movements; thus, it is not clear if

* Corresponding author. Tel.: +1 902 494 1164; fax: +1 902 494 5120.
E-mail address: david.westwood@dal.ca (D.A. Westwood).
URL: www.actionlab.ca (D.A. Westwood).

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reaching movements derive any (perhaps minimal) performance benefit when the eyes are allowed to move to the target first. In the present study we compare reaching movements with and without concurrent eye movements. Furthermore, the upper limb was visible in Bernardis et al.'s study, so participants may have been able to detect and correct reaching errors by comparing the position of the limb to stable visual landmarks present in the environment. Here we blocked vision of the upper limb using a mirrored apparatus.

If the resistance of reaching movements to the ML illusion depends at all on the engagement of the oculomotor system, then reaching endpoints should be less sensitive to the illusion in the hand + eye condition as compared to the hand-alone condition. The results did not bear out this prediction; reaching endpoints were not affected by the illusion in either condition, and there was no reduction of the illusion's effect in the hand + eye condition. Participants in the study were right-handed ($N = 12$; 5 male, 7 female) between the ages of 21 and 45 years (mean: 26 ± 7 years) with no history of visual or motor dysfunction. Participants provided informed consent, and were treated in accordance with the ethical guidelines of Dalhousie University's Human Research Ethics Board.

Stimulus arrays consisted of a single red target circle (1° in diameter) presented in one of three versions of a Müller–Lyer figure (arrow out, arrow in, or "X") drawn using black circles of the same dimension as the target (Fig. 1). The target circle was located either 19 or 21 cm (19° or 21°, based on the viewing distance of approximately 57 cm) to the left of a fixation point that was aligned with the body midline.

Stimuli were presented using a 19″ LCD monitor inverted 30 cm above a half-silvered mirror which was in turn mounted 30 cm above a table surface oriented in the horizontal plane. Participants viewed the reflected image from the monitor by looking

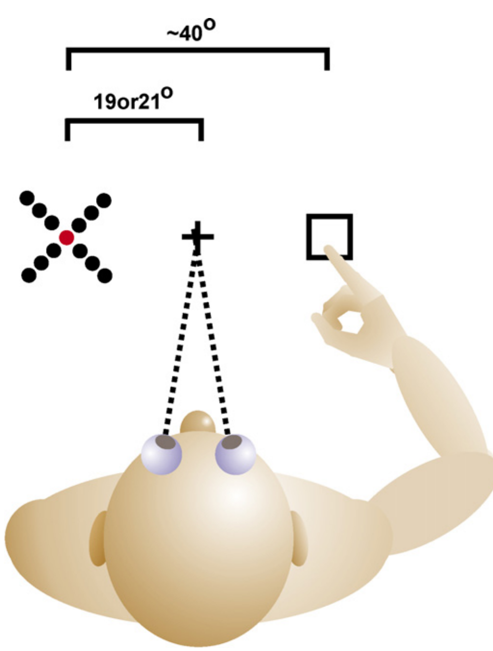

Fig. 1. Schematic illustration of the stimulus display. Stimulus, hand, and target locations were common at the start of all perceptual and motor tasks.

downwards into the half-silvered mirror, creating the perception of an image located on the table surface below. The space beneath the half-silvered mirror was not illuminated, rendering the arm invisible beneath it.

In the perceptual task, participants verbally reported the distance of the target relative to the fixation point, while holding their gaze at the fixation point (data from trials in which the eyes moved away from fixation were discarded). Target distance was reported using a scale of 0–10, where "10" was the distance to the farthest edge of the display and "0" was the centre of the fixation point.

In three separate blocks of trials, participants were required to (1) saccade to the target ("eye-only" trials), (2) reach to the target ("hand-only" trials), or (3) reach and saccade to the target ("eye + hand" trials). Half of the participants completed the perceptual task before the three motor tasks, and the other half completed the three motor tasks before the perceptual task. The order of motor tasks was counterbalanced. Participants were instructed to move as quickly and accurately as possible in all conditions. In all trials the eyes started at the fixation point and the right finger started at the home switch position. For the eye + hand trials, no specific instructions about the sequencing of eye and hand movements were given to ensure a natural temporal coordination of these movements.

Hand movements were measured using a miniBIRDs® 500 (Ascension Technology Corporation, Burlington, VT) magnetic position tracker (sampling rate = 103.3 Hz), and eye movements were measured using an EyeLink®II (SR Research Ltd., Mississauga, ON) video-based eye-tracking device (sampling rate = 500 Hz; spatial precision <0.01°; spatial accuracy <0.8° RMS error). Calibration of the EyeLink II was carried out in the same horizontal viewing plane that was used to display the target stimuli.

At the start of each trial, participants held gaze on the fixation point and held down a starting switch in the table 30 cm in front of the chest, and 20 cm to the right of the body midline. The stimulus array was presented 500–1500 ms after the hand and eyes were appropriately positioned; this fore period varied randomly from trial to trial. The onset of the stimulus was the participant's cue to respond. Prior to stimulus onset, trials were aborted if the participant's gaze deviated from the fixation point or if the finger released the start button. The fixation point remained visible throughout the trial, as did the stimulus array. The trial ended 2500 ms after target onset.

There were a total of 96 trials in the experiment, 4 trials for each of the 6 stimulus arrays (i.e., 2 target locations by 3 illusion configurations) in the perceptual task and 4 trials for each of the 6 stimulus arrays in each of the 3 motor tasks (i.e., eye-only trials, hand-only trials, and eye + hand trials).

Dependent measures for reaching movements were reaction time (RT), movement time (MT), spatial endpoint in the primary (horizontal) movement axis, peak hand speed, time to peak hand speed, peak hand acceleration, and time to peak hand acceleration. Dependent measures for the primary saccades were reaction time (RT), movement time (MT), and horizontal gaze position. In addition, the position of the gaze at the end of the secondary saccade (if one was present) was also analyzed; note that we did