The induced Roelofs effect: two visual systems or the shift of a single reference frame?

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Abstract

Cognitive judgments about an object's location are distorted by the presence of a large frame offset left or right of an observer's midline. Sensorimotor responses, however, seem immune to this induced Roelofs illusion, with observers able to accurately point to the target's location. These findings have traditionally been used as evidence for a dissociation of the visual processing required for cognitive judgments and sensorimotor responses. However, a recent alternative hypothesis suggests that the behavioral dissociation is expected if the visual system uses a single frame of reference whose origin (the apparent midline) is biased toward the offset frame. The two theories make qualitatively distinct predictions in a paradigm in which observers are asked to indicate the direction symmetrically opposite the target's position. The collaborative findings of two laboratories clearly support the biased-midline hypothesis.
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Keywords: Localization; Direction; Illusion; Perception; Action

1. Introduction

Common experience implies that vision is a unified sense, with all of its capabilities tied together in a single, coherent whole. Perceived positions of objects and surfaces, color, motion, and control of action are smoothly integrated. This intuition contradicts the organization of the brain, however: vision is coded not in one unified area, but in at least two dozen maps of the retina on various brain surfaces, each with its own specialized function (Felleman & Van Essen, 1991).

The juxtaposition of unified perception with multiple physiological maps of visual space has resulted in several theories of the segregation of visual functions. Dominant among these is a theory that divides visual function along two broad lines, one managing visual perception and the other visually guided motor behavior (Bridgeman, Lewis, Heit, & Nagle, 1979). Unity of perception is

achieved because only the perceptual branch supports conscious experience. Following Paillard (1987), who provides other evidence consistent with this conception, the two systems will be called cognitive and sensorimotor, respectively. According to Milner and Goodale (1995), a ventral channel mediates cognition and perception (*what*), while a dorsal channel subserves visually guided behavior (*how*). This dual arrangement allows spatially-directed behavior to be implemented by a dedicated processor operating solely on the here-and-now goal of action. The cognitive pathway specializes in recognizing and remembering the identities of objects and patterns and their spatial interrelationships.

Previous studies have demonstrated a psychophysical method that seems to produce large and consistent contrasts between cognitive and sensorimotor systems, differentiated by response measure (Bridgeman, 1991). This dissociation exploits an illusion, the Roelofs effect: if a rectangular frame is presented off-center, so that one edge is directly in front of the observer, that edge will appear to be offset in the direction opposite the rest of the frame (Roelofs, 1935). With some modification, the Roelofs effect can be applied to investigate the

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two-visual-systems theory (Bridgeman, 1991). First, the frame need not have one edge centered; illusions occur whenever the frame is presented asymmetrically. Second, a target within an offset rectangle is mislocalized in the direction opposite the offset. Thus, the misperception of frame position induces an illusion of target position; this induced Roelofs effect will be called simply a Roelofs effect here.

As developed by Bridgeman and colleagues, the two-visual-systems theory accounted for four phenomena associated with the Roelofs effect. First, a cognitive measure (a verbal response or key press indicating the target's position from among an array of possible positions) produces a Roelofs effect, with the target mislocalized in the direction opposite the frame's offset. Thus, the cognitive system involved in making these symbolic responses (i.e., responses without a 1:1 isomorphic relation to the stimulus position) must encode target location in a manner that is susceptible to distortions caused by the offset frame. Second, the cognitive effect is unchanged by delaying the response, which indicates that the memory representation of the target is similarly susceptible to frame effects. Third, an immediate sensorimotor response (pointing at or jabbing the target) shows no Roelofs effect, suggesting that the sensorimotor system is immune to the distorting contextual cues provided by the offset frame. Fourth, the Roelofs effect appears in the sensorimotor measure after a delay of a few seconds (Bridgeman, Gemmer, Forsman, & Huemer, 2000). This effect could be explained by a lack of memory in the sensorimotor system, forcing that system to import remembered spatial information from the cognitive system, bringing the illusion with it.

Another theory accounting for all four results was recently advanced by Dassonville and Bala (2002; submitted; see also Dassonville & Bala, in press). If the observer's apparent midline or subjective straight-ahead were biased in the direction of the inducing frame in the Roelofs paradigm, then all of the above phenomena would result. [2] The cognitive effect (1) would result from judging target position relative to the biased apparent midline, so that, for instance, a target that is objectively straight ahead will be judged to be to the right of a left-shifted apparent midline. Stability of the cognitive effect with delay (2) occurs because the observer has already chosen a response, and no amount of waiting in darkness will change that opinion. However, if the observer uses the same distorted reference frame to guide the

sensorimotor response (3), the movement would be aimed to the right of the left-shifted apparent midline (just as the target was perceived to lie to the right of the apparent midline) and would therefore be accurate. Reappearance of the Roelofs effect with a delayed sensorimotor response (4) would occur because—with the distorting influence of the frame removed—the apparent midline drifts back to its original position. Since the original target location was perceived to lie to the right of the distorted apparent midline, a delayed response aimed to the right of the now-accurate apparent midline would be in error.

With both the two-visual-systems and biased-midline theories neatly accounting for all four phenomena, theoretical interpretation of the Roelofs effect was at an impasse. What was needed was the 'killer experiment', a condition in which the two theories made distinctly different predictions. Such an experiment had been partially executed unknowingly, about a year before Dassonville and Bala reported their results. Bridgeman and Thiem (unpublished) had in their interpretation tested the limits of the sensorimotor system to represent transformations of spatial information. The task was to jab the screen in the direction symmetrically opposite the target's position (i.e., to a mirror-image location reflected across the apparent midline, Fig. 1A). They measured a huge Roelofs effect—larger than under any conditions in several years of previous work—but could not interpret it and had not published it.

The two-visual-systems theory makes two different predictions in this reflected-motor condition, depending on whether the sensorimotor system can handle the mirror transformation directly or must rely on information in the cognitive system. In its strongest form, the two-visual-systems theory predicts that the accuracy of a pointing movement in the reflected-motor condition should be unaffected by the frame (Fig. 1B). Because the sensorimotor system presumably codes only target position and disregards the Roelofs-inducing frame, motor behavior should be identical in the direct and reflected conditions, except for the reflection about the (objective) midline. A target on the objective midline should elicit identical pointing in the direct and reflected conditions. In a second version of the two-visual-systems theory, the cognitive system would lend its spatial values because the sensorimotor system can code only the target position, not abstract relations between target position and other landmarks such as the midline. This version of the theory predicts a reflected Roelofs effect equal in size to the normal cognitive Roelofs (Fig. 1C).

The prediction of the biased-midline theory is quite different. In the normal sensorimotor condition, the movement is guided within the same distorted reference frame used to encode target location, so the effects cancel. Reflecting the response about a biased apparent midline, however, will cause these errors to sum together

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[2] Dassonville and Bala were not the first to propose that frame-induced distortions of the apparent midline were responsible for the cognitive Roelofs effect (see Bruell & Albee, 1955a, 1955b; Wapner, Warner, Bruell, & Goldstein, 1953). However, those studies did not propose a mechanism by which this distortion could also account for accurate sensorimotor responses, as was done by Dassonville and Bala (2002, submitted).
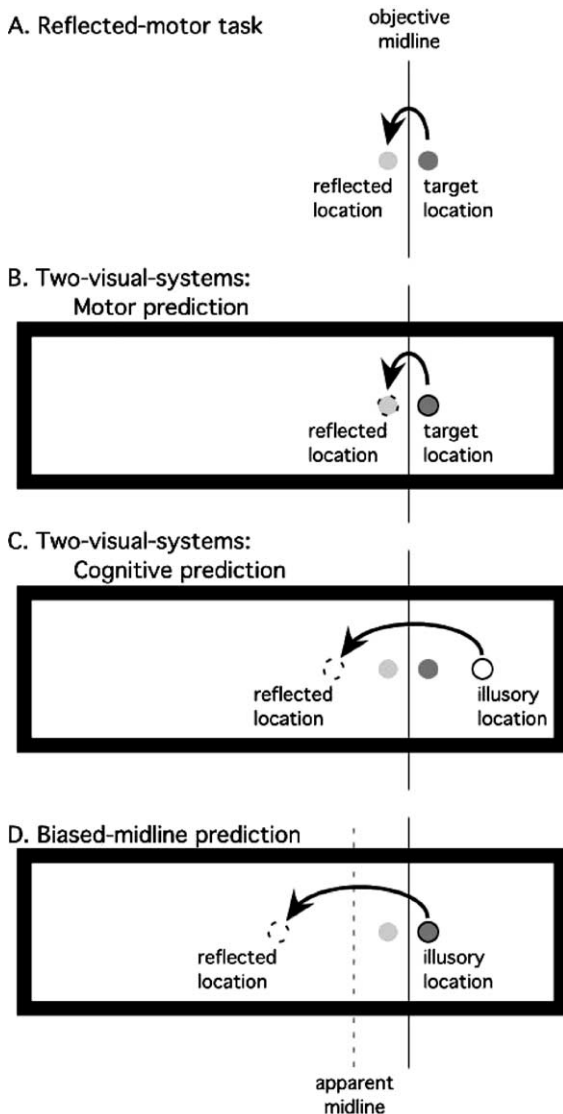
Fig. 1. General spatial layout of the reflected-motor task (A), as well as predictions of the two-visual-systems (B and C) and biased-midline (D) hypotheses. Observers were required to transform the target location (dark gray circle) into its mirror-reflected image (curved arrow) and make a jabbing movement or saccadic eye movement to the unseen reflected location (light gray circle). According to one version of the two-visual-systems hypothesis (B), the motor system would be unaffected by the presence of an offset frame and correctly respond (dashed circle) to the reflected location. If instead the cognitive system was required to perform the mirror transformation (C), the target location would be misperceived (solid circle) and therefore transformed into an incorrect response location, with errors equal in magnitude to the normal Roelofs effect. Alternatively, the biased-midline hypothesis (D) suggests that the target location is mislocalized with respect to the biased apparent midline, with the mirror transformation yielding an error twice the magnitude of the normal Roelofs effect.

instead of canceling, resulting in a doubling of the magnitude of the Roelofs effect (Fig. 1D).

To test these contrasting predictions, reflected-motor experiments were conducted in both the Dassonville and

Bridgeman laboratories, supplemented with measures of standard cognitive and sensorimotor Roelofs effects as well as a measure of bias in the apparent midline in the presence of the inducing frames.

2. Bridgeman experiment

2.1. Method

2.1.1. Observers

Five undergraduate students and one researcher (5 men, 1 woman, all with normal or corrected-to-normal visual acuity) volunteered to participate.

2.1.2. Apparatus

Observers sat in darkness, with their heads stabilized using a chin rest. A touchpad was positioned in the frontal plane, an arm's length from the observer. A mirror mounted at a 45° angle both blocked the observer's view of the touchpad and reflected the image of a horizontally mounted computer display such that stimuli on the display appeared at the same distance and orientation as the touchpad (Fig. 2). Sensorimotor responses were recorded using a cordless stylus, which observers used to jab targets on the touchpad. The stylus was held (using the right hand) with the observer's forefinger on its tip, causing most of the rotation to come from the shoulder of the outstretched arm. Cognitive responses were recorded using five response keys (equivalent to a press on a keyboard). A computer controlled trial presentation and data collection (i.e., the response location of the jabs).

2.1.3. Stimuli

Stimuli consisted of three rectangular frame positions crossed by three target locations. The frame (white, 20°×10°, 1° thick) was either centered on the observer's midline, 4° left of center, or 4° right of center. A target was a vertically symmetrical, yellow insect approximately
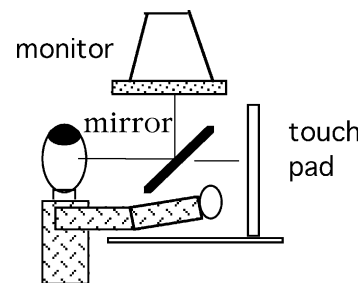

Fig. 2. Layout of the equipment for visual presentation and response collection in the Bridgeman laboratory. The angled mirror allows the monitor display to appear at the distance and orientation of the touchpad, in a frontoparallel plane.

1° high and 0.5° wide. Targets were either centered on the midline, or 4° left, or 4° right of center. Both the frame and the targets were displayed on a black computer screen so as not to give observers any point of reference.

2.1.4. Procedure

2.1.4.1. Cognitive measure. *Training.* Observers were shown five possible target locations (−4°, −2°, 0°, 2°, and 4° from midline, although only the targets at −4°, 0° an 4° were presented during subsequent test trials) in sequence on blank space. This procedure was repeated three times.

Test. The stimulus presented on each trial was chosen randomly without repetition. Once all 9 (3 frame positions × 3 target locations) had been presented, the presentations were re-randomized and the process repeated. Observers were given five presentations of each condition for a total of 45 trials. Rest periods were provided, with the room illuminated. Each stimulus (consisting of a target within a frame) remained displayed for 1 s. Observers were instructed to estimate the target position immediately after each stimulus had disappeared from the monitor by pressing one of the five response keys (open-loop) associated with the possible target positions learned during training.

2.1.4.2. Sensorimotor measure. *Training.* Prior to the testing phase, observers underwent a training phase until they were judged by the experimenter to be comfortable with the task (about 5–10 trials on average). Trials in the training phase were exactly like those in the test phase.

Test. Observers were instructed to hold the stylus with their index finger pointing forward. They were asked to jab the target (as if they were squashing an insect) and to respond as quickly and accurately as possible after its offset. Presentations of the stimuli followed the same pattern as the cognitive measure.

2.1.4.3. Reflected-jab measure. The reflected-jab task was identical to the sensorimotor task, except that observers were instructed to jab an equal distance from the midline in the direction opposite the location of the target (instead of jabbing directly the target as they did in the sensorimotor task).

2.1.4.4. Straight-ahead measure. Observers were instructed to ignore the stimulus and jab in accord with their midline, in the same fashion as they jabbed in the motor and reflected-jab tasks (although the aim of their jabs was directed toward something different in each of the three conditions). They jabbed for fifteen trials with the stimuli present and fifteen trials in blank space.

2.1.5. Analysis

Data from six observers in all four experimental conditions were analyzed with a mixed design ANOVA with observer as a between-subjects factor and frame and target positions as repeated-measures factors. Each observer ran under all conditions. Three levels of frame and target position (−4°, 0°, and +4° of visual angle) created a 3×3 factorial design. The cognitive, sensorimotor, and reflected-jab conditions included five presentations of all stimulus combinations resulting in 45 trials each. Data were analyzed offline with SAS/STAT 6.12. The dependent variable was position of response in visual angle along the horizontal axis. An overall significant ANOVA preceded planned comparisons (*t*-tests for matched pairs) for the theoretically relevant conditions. Roelofs effects were measured as main effects of frame on the dependent variable. To determine amplitudes of Roelofs effects, data from the frame-left and the frame-right conditions were compared, disregarding the frame-center trials. In order to minimize any distortions from edge effects, data were considered only from trials in which the target was objectively centered.

2.2. Results

Results from the cognitive and sensorimotor conditions replicated previous findings on the Roelofs effect (Bridgeman et al., 2000; Bridgeman, Peery, & Anand, 1997). Specifically, a significant main effect for frame position ($t_{(5)} = 6.52$, $p = 0.0013$) revealed a Roelofs effect in the cognitive task, while none was seen in the sensorimotor task ($t_{(5)} = 1.47$). The reflected-jab response also showed a significant main effect of frame position ($t_{(5)} = 7.65$, $p = 0.0006$).

The crucial comparison in differentiating between the two-visual-systems and biased-midline theories is between the magnitude of the Roelofs effect for the cognitive and reflected-jab responses (Fig. 3A). Amplitude of the reflected Roelofs effect was significantly larger than the amplitude of the cognitive effect ($t_{(5)} = 2.60$, $p = 0.048$), but was not statistically significantly different from twice the amplitude of the cognitive effect ($t_{(5)} = 0.022$). This pattern was generally true across the individual observers, as demonstrated by a regression of reflected responses against cognitive responses (Fig. 4A), with a slope (1.80; $R^2 = 0.84$, with the function forced through the origin) that was significantly greater than 1 ($t_{(7)} = 2.27$, $p = 0.036$), but was not significantly less than 2 ($t_{(7)} = 0.55$).

In the straight ahead jabbing task, there was a significant main effect for frame position ($t_{(5)} = 4.12$, $p = 0.0092$). As expected, this effect of 1.21° was in the direction opposite the normal Roelofs effect; that is, straight-ahead jabs tended to deviate to the same side as the frame, as has been reported by Dassonville and Bala (2002, submitted) for saccadic eye movements.
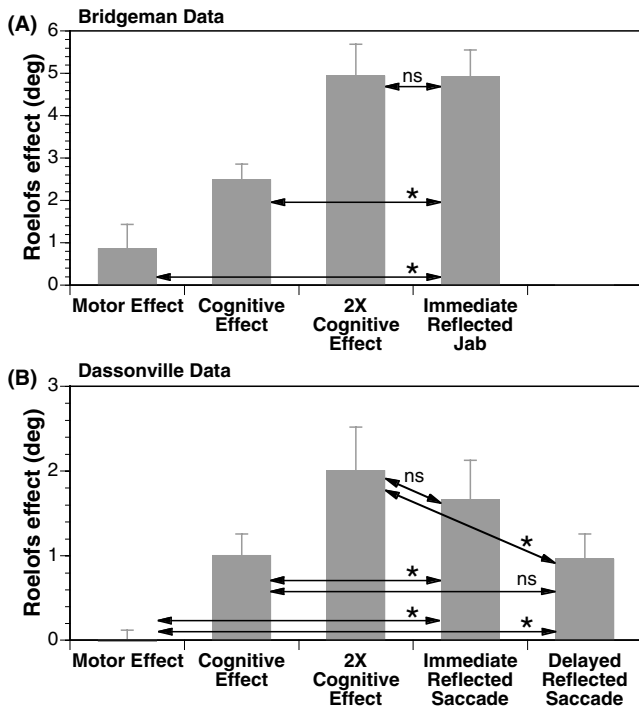
Fig. 3. Comparison of Roelofs effect magnitudes under all experimental conditions, as measured by the Bridgeman (A) and Dassonville (B) labs. Magnitude of the effect was measured as the difference in localization for left-offset and right-offset frames, with positive values indicating a mislocalization in the direction opposite the frame offset; for ease of comparison, data for the reflected-motor tasks have been inverted by multiplying with −1. Data for the motor effect displayed in (B) were collected by Dassonville and Bala (2002, submitted). Asterisks depict significant differences ($p < 0.05$; ns = not significant).
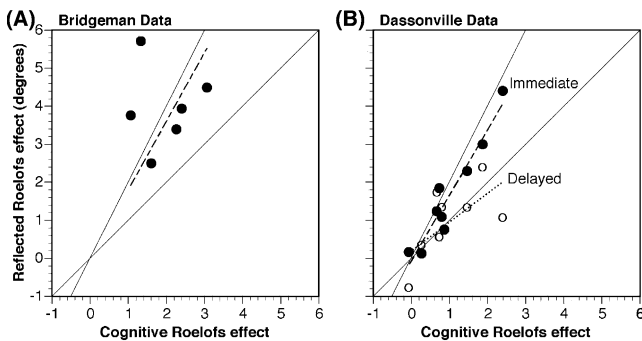

Fig. 4. Regression of the reflected-motor Roelofs effect versus the cognitive Roelofs effect, as measured in the Bridgeman (A) and Dassonville (B) labs. For comparison, the thin solid lines depict slopes of 1 and 2. The dashed lines are the least-squares linear fit to the data from the reflected-motor tasks with immediate responses, while the dotted line is the linear fit to the reflected-motor data with delayed responses (measured only in the Dassonville lab).

3. Dassonville experiment

Concurrent with the collection of data in the Bridgeman laboratory, a similar (but not identical) experiment was run in the Dassonville laboratory. Unlike the

Bridgeman version of the task, observers used saccadic eye movements rather than jabbing movements to indicate the reflected location of the target. In addition, observers made these reflected saccades either immediately or after a 5 s delay from stimulus offset. The observers' sensorimotor abilities to indicate the actual target location and the apparent midline were not assessed (see instead Dassonville & Bala, 2002, submitted).

3.1. Method

3.1.1. Observers

Nine undergraduate students at the University of Oregon (7 men, 2 women, all with normal or corrected-to-normal visual acuity) provided informed consent before participating. Each was compensated with a small monetary payment.

3.1.2. Apparatus

Observers were placed in a darkened room, and viewed a visual display that was back-projected (Barco Cine7 projector) onto a flat screen (128×96 cm^2) located 122 cm from the eyes. Cognitive responses to indicate target location were made by pressing one of five keys on a computer keyboard. For sensorimotor responses, binocular gaze was measured at 240 Hz (Eyelink, Sensomotoric Instruments), with the average of the signals from the two eyes providing a single measure of gaze direction.

3.1.3. Stimuli

Visual targets (0.35° diameter red spot, located −4, −2, 0, 2 or 4° from midline at eye level) were presented within a large red frame (21° horizontal × 8.5° vertical, 1° in width) that was either centered with respect to the observers' midline, or shifted 5° left or right of midline. Frames were presented for 1 s, with targets appearing only during the last 100 ms of the frame duration.

3.1.4. Procedure

Each observer participated in two separate experimental sessions—one to measure the effect of the Roelofs illusion on cognitive judgments and the other to measure the effect on reflected saccades.

3.1.4.1. Cognitive measure. Training. Observers were first shown the array of five possible target locations, and then were presented single targets to be identified by pressing the appropriate response key (using the right hand, the thumb indicated the left-most target position, the little finger indicated the right-most location, etc.). Each trial started with the presentation of a fixation point (8.5° above eye level, at the observer's midline). After moving the eyes to the fixation point, the observer began each trial by pressing the spacebar of the response keyboard, which caused the fixation point to be extinguished. After a random delay (1250–1750 ms), one of

the targets was presented (100 ms duration, with no frame presented), and the observer immediately responded by pressing the appropriate response key. After each trial, feedback was provided by a re-presentation of the target and a computer-generated verbal report of accuracy (accurate responses were reported as being "Correct", whereas incorrect responses generated a report that the response was "Wrong", followed by the location that should have been reported). Observers were required to maintain fixation within 2° of the fixation location throughout the duration of the trial, even after the disappearance of the fixation point. Training continued until observers performed 20 correct responses.

Test: Test trials were identical to training trials, except that (1) no feedback on accuracy was provided, and (2) the target was presented within the large centered or offset frame. Frame presentation (1 s duration) began after a random delay of 350–850 ms from fixation point offset, with the target duration (100 ms) overlapping the last 100 ms of the frame duration. Six blocks of trials were presented to each observer (90 trials total), with each block comprising 15 trials (3 frame positions × 5 target locations) presented in random order without repetition. Trials were aborted and repeated later in the experiment if the eyes left the 2° invisible fixation window before the trial's end.

3.1.4.2. Immediate and delayed reflected-saccade measures.

Training. In a separate experimental session, the same observers were trained to respond to the target by making a saccade to a location an equal distance from the midline in the direction opposite the location of the target. Observers were instructed to withhold the saccadic response until a computer-generated voice provided the command to "Respond," which was timed to occur either simultaneous with the target presentation or after a 5 s delay. Upon fixating the desired reflected location, observers ended the trial by pressing the 'Enter' key of the keyboard. During training, feedback on the accuracy of each response was provided by presenting a visual cue (small circle) at the reflected location, as well as a cue (small square) indicating the eyes' position at the end of the trial. Observers were instructed that the distance between these feedback cues represented the magnitude of the error, and were asked to attempt to minimize this error. Practice trials were continued until the experimenter subjectively noted a stabilization in the magnitude of the observer's errors.

Test. Test trials were identical to the training trials, except that the target was presented within the large centered or offset frame, and no feedback on accuracy was provided. Six blocks of trials were presented to each observer (180 trial total), with each block comprised of 30 trials (3 frame positions × 5 target locations × 2 delays) presented in random order without repetition.

Trials were aborted and repeated later in the experiment if the eyes left the 2° invisible fixation window before the computer-generated "Respond" command.

3.1.5. Analysis

Response errors were analyzed with an ANOVA (SPSS, Inc.), using experimental condition (cognitive measure, immediate reflected-saccade, delayed reflected-saccade), frame position and target position as repeated measures, yielding a $3 \times 3 \times 5$ factorial design. To measure the effects of frame position, data from the frame-left and the frame-right conditions were compared across all target locations. To allow for a comparison of the errors made in the cognitive and reflected-saccade tasks, the sign of the errors in the reflected-saccade tasks was inverted by multiplying with -1.

3.2. Results

Across all tasks, there were main effects of frame location ($F_{(2,14)} = 12.07, p = 0.0009$) and target location ($F_{(4,28)} = 16.41, p < 0.0001$). Importantly, there was also a significant frame × task interaction ($F_{(4,28)} = 3.093, p = 0.0315$). Tests of within-subjects contrasts found the frame effect to differ significantly between the cognitive and immediate reflected-saccade tasks ($F_{(1,7)} = 10.1, p = 0.0155$), but no differences were found between the cognitive and delayed reflected-saccade tasks ($F_{(1,7)} = 0.011$).

When tested separately, each experimental condition was found to have a significant effect of frame position (cognitive: $F_{(2,16)} = 10.57, p = 0.0011$; immediate reflected-saccade: $F_{(2,16)} = 10.01, p = 0.0015$; delayed mirrored-saccade: $F_{(2,16)} = 9.80, p = 0.0084$). Consistent with the within-subjects contrasts reported above, however, the magnitude of this effect did differ between the conditions (Fig. 3B). A statistical comparison revealed that the effect for the immediate reflected-saccade condition was significantly greater than that of the cognitive condition ($t_{(8)} = 2.86, p = 0.021$) but did not significantly differ from twice the effect of the cognitive condition ($t_{(8)} = 2.25$). A regression of the effects from the immediate reflected saccades and the cognitive measure in each observer resulted in a slope of 1.72 ($R^2 = 0.92$; Fig. 4B), which was significantly greater than 1 ($t_{(7)} = 3.69, p = 0.0039$), but was not significantly less than 2 ($t_{(7)} = 1.43$).

The opposite pattern was seen when comparing the delayed reflected-saccade and cognitive effects. The mean effect of the delayed reflected-saccade condition did not differ from that of the cognitive condition ($t_{(8)} = 0.18$), but was significantly different from twice the effect of the cognitive condition ($t_{(8)} = 2.64, p = 0.030$; Fig. 3B). Similarly, a regression of the effects from the delayed reflected-saccades and the cognitive measure in each observer resulted in a slope of 0.76

($R^2 = 0.43$; Fig. 4B), which was not significantly different from 1 ($t_{(7)} = 0.73$), but was significantly less than 2 ($t_{(7)} = 3.74$, $p = 0.0036$).

4. Discussion

The reflected-motor paradigm presented here provided an opportunity to clearly distinguish between two possible explanations for the cognitive and sensorimotor effects of the Roelofs illusion. Whereas the two-visual-systems theory predicted a Roelofs illusion of normal magnitude in this paradigm, the biased-midline theory predicted an effect twice the normal magnitude. Data from both labs clearly indicated that the effect was very nearly twice the normal Roelofs illusion, regardless of the effector (eye or hand) used. Thus, the prediction of the biased-midline theory was upheld, confirming the findings of Dassonville and Bala (2002, submitted). The combined data also show that the effects are robust, not dependent on the specifics of training, stimulus timing and geometry, motor response modality, configuration of simultaneously measured conditions, or small differences in analytical methods.

While the immediate reflected-motor responses demonstrated that target positions are encoded with respect to a malleable apparent midline, trials with delayed responses provided evidence that the frame's effect on the apparent midline is relatively short-lived, with the mislocalizations decreasing during the 5 s delay after frame offset. This is expected if one assumes that, after the frame is removed, its distorting influences decrease over time. However, one should not assume that, since the delayed responses still showed errors half as large as the effect seen with immediate responses, the apparent midline had drifted only halfway back toward its veridical location after 5 s. Consider an example in which the target is presented directly in front of the observer, in the presence of a left-shifted frame. The frame will pull the apparent midline to the left, causing the observer to perceive the target to be located to the right of perceived straight ahead, with the reflected-location an equal distance to the left of perceived straight ahead (Fig. 5A). After the frame is removed, the apparent midline will drift back toward veridical (Fig. 5B), perhaps under the influence of proprioceptive cues (Karnath, 1999). If the remembered target and its mirror-reflected location are encoded with respect to the apparent midline during this memory period, their subjective locations would also drift to the right. In this way, the remembered target location would now appear to the right of its original veridical location (as was demonstrated by Dassonville & Bala, 2002, submitted), while the remembered reflected position would be located to the left. With a delay long enough to allow the apparent midline to drift back to its veridical position, observers would mislocalize the re-
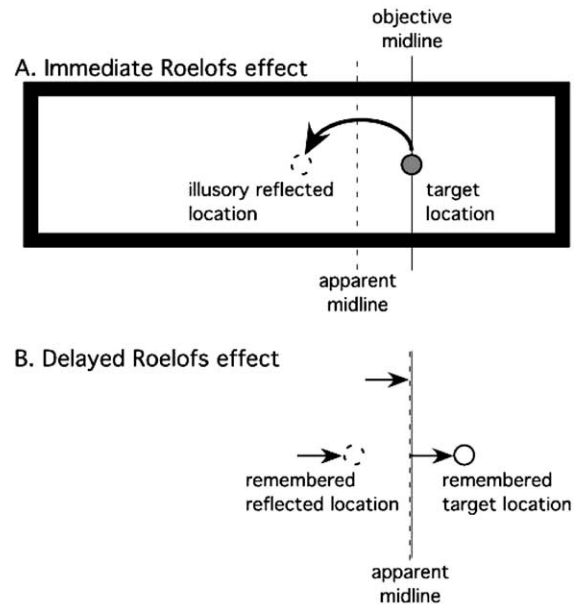

Fig. 5. Schematic describing the proposed mechanism to explain the differences in Roelofs effect for immediate (A) and delayed (B) reflected-motor responses. Immediate responses (A) would be guided to an illusory mirror location (dashed circle) defined by the relationship between the target location and the distorted apparent midline, resulting in an error twice the magnitude of the normal Roelofs effect (as described in Fig. 1). During a delay (B), however, the apparent midline would drift back toward the objective midline, dragging with it the memory of the target (solid circle) and its reflected location, eventually resulting in an error equal in magnitude to the normal Roelofs effect.

flected position with an error equal to the normal Roelofs effect (as was seen in the present data). Thus, the data presented here support the hypotheses that the apparent midline drifts back to its veridical orientation after the distorting influence of the frame is removed, and that remembered target locations are encoded with respect to this malleable apparent midline (Dassonville & Bala, 2002, submitted; see also Mergner, Nasios, Maurer, & Becker, 2001).

Further support for the biased-midline hypothesis was provided by direct measurements in the Bridgeman lab of the observers' apparent midline (measured by asking the observers to point straight ahead), revealing a frame-induced distortion similar to that shown previously by Dassonville and Bala (2002, submitted) using saccadic reports. This was not the first time that the Bridgeman group considered the possibility of a midline distortion as the underlying cause of the Roelofs effect. Indeed, this possibility was tested by Bridgeman et al. (1997, experiment 3) in a task that was conceptually very similar; however, the results at that time indicated no distortion of the apparent midline. The exact cause for the discrepancy between the early negative findings and these more recent findings is unclear, but we can offer a few speculative reasons. First, whereas Dassonville and Bala

(2002, submitted) and Bridgeman in the current study asked observers to perform the egocentric tasks of looking or pointing straight ahead in complete darkness, Bridgeman et al. (1997) had asked observers to perform an exocentric (allocentric) task of pointing to *the center of the apparatus* used to display the visual stimuli (a large, bright hemicylindrical screen). The observers in the earlier experiment may have used visible landmarks (e.g., the edges of the 180 deg screen seen with eccentric gaze in peripheral vision) to determine the center of the apparatus in spite of a biased apparent midline. Second, observers in the task of Bridgeman et al. (1997) provided a motor report by swinging a pointer so that its tip indicated the desired location. Since the pivot point for this pointer lay just in front of the observer's chest, it is possible that observers used proprioceptive information about the pointer's angle in space as a cue for straight ahead; that is, observers might have relied on a strategy of turning the pointer until its shaft was aligned perpendicular to the frontoparallel plane of the body. The paradigms of the present study and that of Dassonville and Bala (2002, submitted) required observers to make open-loop jabbing and eye movement responses in complete darkness, eliminating these potential confounding cues.

Although the effect of the frame on the direct measurement of the apparent midline was significant, it was smaller in magnitude (1.21°) than the cognitive Roelofs effect similarly measured in the Bridgeman lab (2.47°; $t_{(5)} = 3.71$, $p = 0.014$). This difference may be accounted for by the manner in which the transient nature of the midline distortion differently affects the cognitive and sensorimotor responses. As described above, any delay in the observer's jabbing response (as measured from the offset of the frame) will provide some time during which the apparent midline will drift back toward the objective midline. This change would be irrelevant for cognitive judgments about target position, since these judgments would undoubtedly be made very near to the time of target presentation, regardless of when the observer's overt response is actually performed. However, the Roelofs effect for movements to indicate the apparent midline would shrink during a delay (perhaps even a delay as short as a normal reaction time), even while the effect would grow for movements to indicate the position of a target presented within the frame (Fig. 5B). While the time course of these changes is still not well understood, a significant change is apparent with a delay of 1 s (Bridgeman et al., 2000), and is not yet complete even after 5 s (Dassonville & Bala, 2002, submitted). Given this, it is expected that a direct measurement of a frame's effect on the apparent midline will generally underestimate the magnitude of the Roelofs effect, if the observer's response occurs after the frame is removed from view. However, since the time course of the change in the apparent midline is expected to mirror that of the change in a remembered target's location (Fig. 5b), the

difference between these two should always equal the magnitude of the Roelofs effect, regardless of the delays at which they are measured. Indeed, as measured in the Bridgeman lab, this difference of 2.06° does not significantly differ from the magnitude of the cognitive Roelofs effect ($t_{(5)} = 1.47$).

The biased-midline hypothesis has been proposed previously as a mechanism which neatly accounts for the previously-described cognitive illusion of the Roelofs effect (Bruell & Albee, 1955a, 1955b; Wapner et al., 1953), as well as the motor effects seen when observers point or look straight ahead or to a remembered target (Dassonville & Bala, 2002, submitted). The results of the present study further confirm that the apparent midline is biased by the presence of an offset frame, and they delineate yet another type of sensorimotor response (i.e., eye and hand movement to a mirror-reflected target) that is affected by this distortion. The results presented here, however, do not *definitively* rule out a very weak form of the two-visual-systems hypothesis, in which a cognitive system is affected by a distortion of the apparent midline while a separate motor system, immune to this distortion, is responsible for guiding only those movements aimed immediately and directly toward a visible target. For this form of the two-visual-systems hypothesis to be viable, though, the function of this proposed motor system must be extremely limited, being dependent on a cognitive system to guide eye and hand movements to indicate the straight-ahead direction, as well as movements aimed at remembered targets or those defined allocentrically. Furthermore, the functional abilities of this proposed motor system would be redundant with those of the cognitive system (at least with respect to the Roelofs effect), as evidenced by the fact that movements aimed at allocentrically-defined targets—which are presumed to be guided by the cognitive system within the two-visual-systems framework (Dijkerman, Milner, & Carey, 1998)—are unaffected by the Roelofs effect just as are movements aimed toward a visible target (Dassonville & Bala, submitted).

In contrast, the biased-midline hypothesis can mechanistically explain all of the perceptual and sensorimotor effects of Roelofs illusion (including the *absence* of a Roelofs effect for movements guided to targets that are present when the movement is initiated) and it does so without requiring the assumption of separate but redundant maps of space for cognition and action. Given this, we conclude that the behavioral dissociations associated with Roelofs illusion should no longer be considered as exclusive evidence for the two-visual-systems hypothesis.

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