

Combined effects of feature-based working memory and feature-based attention on the perception of visual motion direction

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We investigated whether human subjects' ability to identify the direction of a brief pulse of coherent motion in a random-dot pattern (RDP) was influenced by: (a) maintaining in working memory the direction of motion of an RDP previously presented far from the pulse (feature-based working memory or FBWM, [Experiment 1](#)), (b) attending to the direction of an RDP co-occurring with but far from the pulse (feature-based attention or FBA, [Experiment 2](#)), and (c) both FBWM and FBA acting simultaneously ([Experiment 3](#)). In the first two experiments, pulse direction identification performance was higher when the remembered direction (FBWM) or the direction of the concurrently attended RDP (FBA) matched the pulse direction than when it was opposite. In [Experiment 3](#), performance was highest when both the remembered and the attended directions matched the pulse direction (combined effects of FBWM and FBA), it was intermediate when only one of them matched the pulse direction, and it was lowest when neither matched the pulse direction. Our results demonstrate that both feature-based working memory and feature-based attention can individually modulate the perception of motion direction and that when acting together they produce an even larger modulation.

Keywords: working memory, feature-based attention, motion perception, motion direction, psychophysics

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Introduction

The human visual system faces at least two major challenges concerning information processing. First, the amount of information that enters the retina at any given moment greatly exceeds the system's processing capacity. Second, visual information often becomes unavailable while it is still relevant to behavior. Two cognitive processes provide solutions to these challenges. The first, attention, allows us to select behaviorally relevant visual signals and enhance their processing, while filtering out irrelevant ones (Boynton, 2005; Posner, 1980). The second, working memory (WM), allows us to temporarily maintain representations of behaviorally relevant stimuli that are no longer visible (Baddeley, 1996; Goldman-Rakic, 1995; Postle, 2006). After decades of research in vision, it remains largely elusive how these two processes interact (Awh, Vogel, & Oh, 2006).

A widespread conception in cognitive science is that the attentional control system is one of the key elements of WM (Baddeley, 1996). At the same time, it has been hypothesized that WM representations are linked to the origin of attentional signals. For example, it has been proposed that top-down attentional filtering might result from the effect of WM representations of behaviorally relevant features (e.g., spatial location, color, shape) modulating the processing of retinal signals in visual cortical areas (Desimone & Duncan, 1995). Strong evidence in favor of this proposition has come from neurophysiological studies of visual search in monkeys (Bichot & Desimone, 2006; Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993, 2001). Visual search tasks, however, require a template item in WM to intentionally guide the search toward matching items on a display. A generalization of the concept of WM-guided attention has further led to the hypothesis that the maintenance of visual representations

in WM than pulses in the opposite direction (effect of FBWM).

Methods

Subjects

Seven subjects (2 females, 5 males) aged between 20 and 40 years (median = 27 years) with normal or corrected-to-normal vision participated in the study. Four of them were naïve to the purpose of the experiment. Each subject gave written consent prior to the experiments. All procedures were preapproved by the Ethics Committee of the Faculty of Medicine at McGill University.

Each of the seven subjects completed Experiments 1, 2, 3, and Controls in three sessions of approximately 45 min each. Every subject performed a total of approximately 300 trials: 30 in Experiment 1, 40 in Experiment 2, 60 in Experiment 3, 60 in Control 2, 50 for the estimation of the psychometric curve of pulse coherence, and between 15 and 35 practice trials for each experiment. Five of these subjects also participated in Experiment 4. Two additional subjects participated in Experiments 3 and 4.

Setup and stimuli

During the experiments, each subject sat in a dark room 57 cm away from a CRT computer monitor (LaCie, Oregon, USA, 75-Hz refresh rate, 1280 × 1024 resolution, size 21 inches). The subject's head was stabilized using a head–chin rest. The experiments and stimuli were programmed using the Matlab Psychophysics Toolbox software (Mathworks, Naticks, MA), running on an Apple G4 PowerPC computer (Apple, Cupertino, CA). Stimuli were displayed on a dark background (luminance < 0.001 cd/m²) and consisted of a 0.25°-by-0.25° fixation square located in the middle of the screen, a 0.93°-by-0.13° horizontal bar (spatial cue) located 2.80° to the left or right of the fixation square, and random-dot patterns (RDPs; Figure 1). Each RDP was composed of 300 white dots (luminance of 39.75 cd/m²). The dots were 0.09° in diameter and moved at a speed of 4.7°/s in linear trajectories within a stationary virtual circular aperture of 6.25° in diameter. RDPs were presented centered at 3 locations: sample, pulse, and test. The sample location was 5.63° above the fixation square. The test location was 9.38° toward one side of the fixation square. The pulse location was 9.38° away from the fixation square, on the side opposite to the test location. In each trial, the test location was randomly chosen as right or left. In order to indicate this location, the spatial cue was displayed during the entire trial. The setup and stimuli properties were the same in all the experiments.

The motion coherence of an RDP was defined as the percentage of dots moving in the same direction (e.g. 50% coherence corresponds to half of the dots moving in the same direction and the remaining dots moving in randomly chosen directions from 0° to 360°). An RDP is

referred to as having 0% coherence if all the dots move in randomly chosen directions (from 0° to 360°). Direction of motion is described relative to the screen's vertical meridian (i.e., upward motion = 0°, rightward = 90°, downward = 180°, and leftward = 270°).

Task

Each trial consisted of two tasks: a delayed match-to-sample task and a pulse identification task (Figure 1). In the delayed match-to-sample task, subjects fixated on the central square at the beginning of each trial, and then pressed the spacebar key to start the trial. One thousand milliseconds later, an RDP appeared at the sample location moving with 100% coherence in one of the following directions: 45°, 135°, 225°, or 315°. After 1000 ms, the sample disappeared and subjects continued fixating for a variable delay period of 1800 to 2250 ms. Following that period, four test RDPs with 100% coherent motion were serially presented at the test location during 250 ms each, separated by intervals lasting from 450 to 750 ms (inter-test intervals). During these intervals, RDPs with 0% coherent motion were presented, as well as before the first and after the last test RDP. Each test RDP could move in a 45°, 135°, 225°, or 315° direction. Subjects were required to count how many of the test directions matched the sample direction. The number of matches could be zero, one, or two and was randomly chosen from trial to trial. Subjects indicated the number of matches at the end of each trial.

In the pulse identification task, subjects viewed an RDP presented at the pulse location from the end of the delayed match-to-sample task delay period until the end of the trial (Figure 1). The RDP contained motion with 0% coherence throughout this entire period except for a 250-ms pulse of coherent motion in a direction of 45°, 135°, 225°, or 315°. The coherence of this pulse was chosen individually for each subject as described in the Data analysis section. Subjects were instructed to identify the pulse direction.

At the end of the trial, all the stimuli were removed and subjects were no longer required to fixate. Four arrows appeared at the screen center depicting the four possible directions of the coherent motion pulse (45°, 135°, 225°, and 315°). Subjects were required to press one of four keys, each corresponding to one pulse direction. Immediately after a response was given, the arrows disappeared and the following text was displayed: “How many matches of sample & test? 0, 1, or 2.” Subjects pressed one of three keys to report the number of matches.

An important detail in this experiment is that the pulse of coherent motion was presented during one of the three inter-test intervals, when only 0% coherent motion was shown at the test location, and while subjects maintained the sample direction in WM in order to perform the delayed match-to-sample task (Figure 1b). This allowed us to test whether the representation of a given direction in WM influenced subjects' ability to identify the direction

of the pulse. In half of the trials, the sample direction was the same as the pulse direction (sample-same condition); in the other half, the sample direction was opposite to the pulse direction (sample-opposite condition).

Randomization procedures

In each trial, we randomly chose the pulse direction, the condition, the directions of the four tests, and the inter-test interval during which the pulse occurred (1st, 2nd, or 3rd). In order to make sure that during the pulse presentation subjects maintained the sample direction in WM, we never presented the pulse after two test directions had already matched the sample (maximum number of matches).

Data analysis

Performance in the delayed match-to-sample task was quantified as the percentage of trials in which a subject correctly reported the number of tests whose direction matched the sample direction. Mean performance across subjects in this task was 92% (88% among sample-same trials and 95% among sample-opposite trials). We excluded from analysis all trials with incorrect responses in the delayed match-to-sample task, since in these trials we could not guarantee that the subjects remembered the sample direction. From the remaining trials, performance in the pulse identification task was measured in each of the two conditions as the percentage of trials in which a subject correctly reported the direction of the coherent motion pulse. In each condition, all subjects performed the pulse identification task above chance.

To correct for deviations from normality and symmetry that may occur in distributions of percentages, we applied a rationalized arcsine transformation on the performance scores. We then compared performance between the two conditions across all subjects by using a paired-samples *t*-test on the transformed data. In all other experiments, statistical tests were also performed on rationalized arcsine-transformed performance values. From now on, we will refer to this transformed data as performance scores or simply performance.

To graph the results across subjects (Figure 3), we normalized the performance of each subject in each condition to the mean performance across conditions. Then, for each condition, we averaged the normalized performances across subjects. The same procedure was used in all other experiments to obtain estimates of mean normalized performance (Figures 5, 7, 8, and 9).

Before starting the experiments, we obtained baseline measurements of each subject's performance in the pulse identification task alone while they were presented with the same pattern of stimuli used in Experiment 1 but were told to ignore the sample and test stimuli. We used five different levels of pulse coherence: 10, 25, 45, 65, and

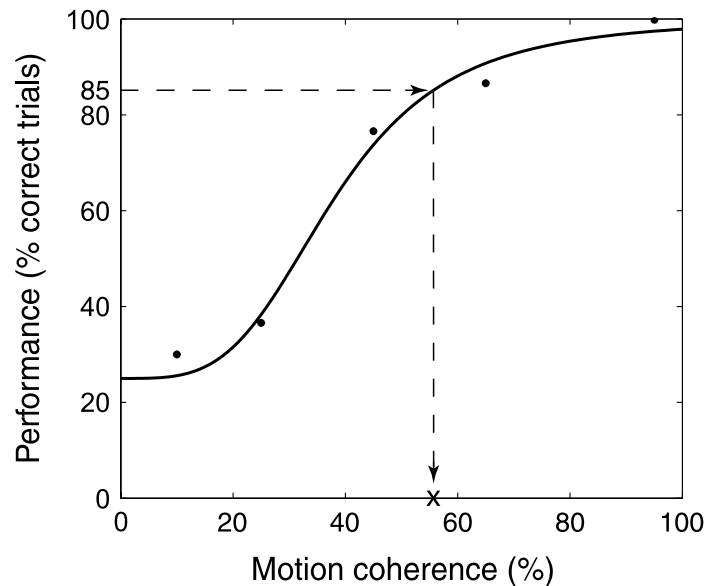


Figure 2. Pulse identification performance of an example subject as a function of motion coherence. The performance data (dots) were fitted with a sigmoid curve. The value of coherence corresponding to 85% performance was calculated from the curve's estimated parameters (dashed lines and X).

95%. Subjects performed a total of 50 trials (10 for each coherence level). Performance data for all five coherence levels were then fitted with the following sigmoid function:

$$P = 100 - 75 \left(\frac{h^s}{h^s + C^s} \right), \quad (1)$$

where C is the coherence level, P is the performance, the parameter h is the coherence value at which half of the curve's performance range is reached (half-maximum), and the parameter s determines the curve's slope at the point of inflection.

We aimed at obtaining from each subject, during Experiments 1, 2, and 3, an average pulse identification performance intermediate between saturation (100%) and chance (25%), ideally in the range of 60% to 70%. We anticipated that performance values in this range would be modulated by FBWM and FBA, while values at saturation or chance may be poorly or not modulated at all by these two factors. We used the pulse coherence level at which subjects perform at 85% during the pulse identification task alone, taking into account that during the dual task performance shall drop at least 15–25% with respect to the single task (Niebergall, Huang, & Martinez-Trujillo, 2010). Thus, for each subject, we used the psychometric curve's fit parameters h and s to estimate the pulse coherence (C) corresponding to 85% identification performance (Figure 2). In all experiments, we set the pulse coherence to this value. Across subjects, the mean

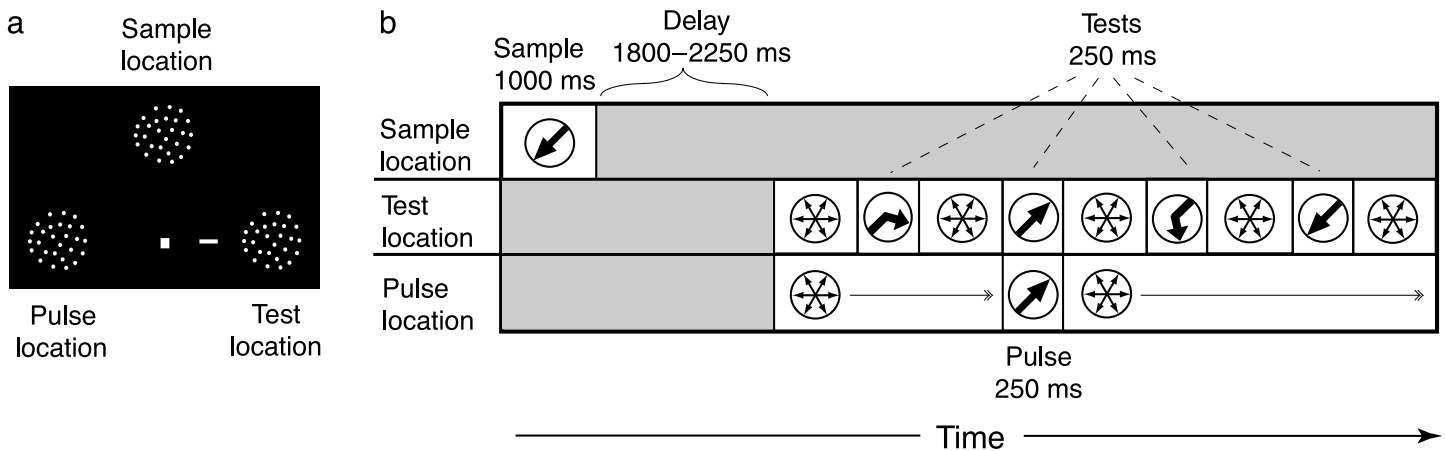


Figure 4. Visual stimuli presented in [Experiment 2](#). (a) Depiction of stimulus display. (b) Diagram showing the time course of stimuli presentation in one sample trial. Subjects performed the direction change detection and the pulse identification tasks simultaneously. Details are as described in [Figure 1](#). Angled arrows represent RDPs that changed motion direction.

at the same time as one of the test stimuli, and (2) either zero, one, or two of the test RDPs were randomly chosen to change their direction of motion by 60° (clockwise or counterclockwise) after 125 ms of presentation ([Figure 4](#)). Two tasks were performed simultaneously in each trial: the direction change detection and the pulse identification task. In the former, subjects had to count how many of the four test RDPs changed direction. As in [Experiment 1](#), a “sample” RDP was presented, but it was irrelevant to the task.

The pulse identification task was the same as that described in [Experiment 1](#). Subjects were required to identify the direction of a 250-ms pulse of coherent motion. The pulse could be presented simultaneously with any of the test RDPs, except with those that changed direction. This avoided exogenous shifts of attention ([Yantis & Jonides, 1990](#)) toward the test stimulus that may influence the amount of attention allocated to the pulse detection task. At the end of each trial, all visual stimuli disappeared and subjects were no longer required to fixate. As in [Experiment 1](#), subjects used key presses to report their choices.

The direction change detection task required subjects to attend to the direction of motion of each of the four test RDPs in order to count the number of direction changes. The pulse RDP occurred while subjects attended to the direction of a test stimulus, allowing us to test whether attending to a particular test direction influenced subjects’ ability to identify the pulse. In 50% of the trials, the pulse and the test had the same direction (test-same condition). In the other 50%, they had opposite directions (test-opposite condition). If FBA—to the motion direction of the test—enhances the perception of motion in that direction, then pulse identification performance in the test-same condition will be higher than in the test-opposite condition.

Randomization procedures

In each trial, we randomly chose the condition, the motion directions of the pulse and the tests, the test with which the pulse co-occurred, the number and order of tests that changed direction, and the direction of the irrelevant sample. Given that subjects could potentially stop attending to the tests after perceiving two direction changes, the pulse never occurred after a second direction change.

Data analysis

We quantified performance in the direction change detection task as the percentage of trials in which a subject correctly reported the number of tests that changed motion direction. Across subjects, mean performance was 86%. Our analysis excluded trials with an incorrect response to the direction change detection task, given that in these trials we could not guarantee that subjects attended to the test stimuli. From the remaining trials, performance in the pulse identification task was independently measured for each of the two experimental conditions (see [Methods](#) section of [Experiment 1](#)).

Results and discussion

We compared pulse identification performance between trials of the test-same and test-opposite conditions. The mean normalized performance across subjects was higher when the pulse and the test had the same direction than when they had opposite directions (paired-samples *t*-test, $t(6) = 1.90$, $p = 0.05$, one-tailed; [Figure 5](#)). Across subjects, performance differed by an average of 13% between the two conditions. Interestingly, this difference was somewhat

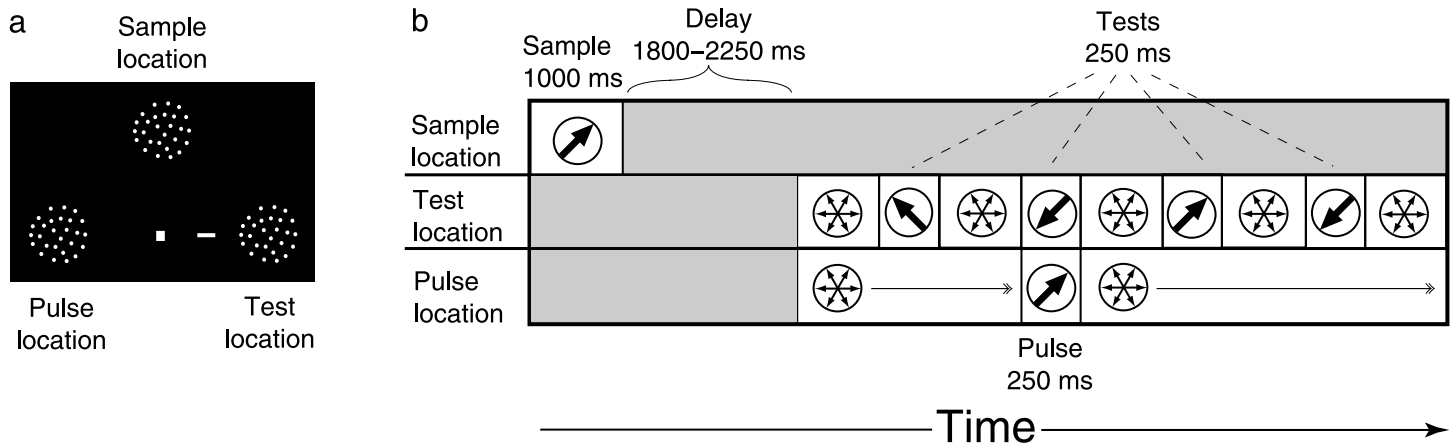


Figure 6. Stimuli in Experiment 3. (a) Depiction of stimulus display. (b) Diagram showing the time course of stimuli presentation in one sample trial. Subjects performed the delayed match-to-sample and pulse identification tasks simultaneously. Details are as described in Figure 1.

During the presentation of the pulse, subjects were required to maintain the sample direction in WM and attend to the direction of the co-occurring test (Figure 6b). To investigate the simultaneous effects of the sample direction (FBWM) and the test direction (FBA) on pulse identification, we designed different trial types based on a two-factorial design. One factor was the direction of the sample with respect to the pulse, which had two levels: sample-same and sample-opposite. The other factor was the direction of the co-occurring test with respect to the pulse, which also had two levels: test-same and test-opposite. The two factors were crossed, resulting in four conditions: sample-same/test-same, sample-same/test-opposite, sample-opposite/test-same, and sample-opposite/test-opposite.

Randomization procedures

In each trial, we randomly chose the pulse direction, the condition, the number of tests with a direction matching the sample, the test directions, and the test with which the pulse co-occurred. The pulse never occurred after two tests matched the sample direction, to make sure that during the presentation of the pulse, subjects were still required to attend to the test and remember the sample direction.

Data analysis

Trials were grouped by condition. For each of the four conditions, the performance of each subject in the pulse identification task was calculated as described in the previous experiments. We did not include trials in which subjects' response to the delayed match-to-sample task was incorrect, since there was no guarantee that in these trials subjects remembered the sample direction and attended to the tests throughout the trial. Across subjects,

mean performance in the delayed match-to-sample task was 88% (87% among sample-same/test-same trials, 91% among sample-same/test-opposite trials, 89% among sample-opposite/test-same trials, and 85% among sample-opposite/test-opposite trials).

Results and discussion

We tested whether pulse identification performance differed across the two levels of each of the factors: the sample direction with respect to the pulse (FBWM) and the co-occurring test direction with respect to the pulse (FBA). The mean normalized performance across subjects was highest in the sample-same/test-same condition, intermediate in the sample-same/test-opposite and sample-opposite/test-same conditions, and lowest in the sample-opposite/test-opposite condition (Figure 7). A two-factor repeated-measures ANOVA across subjects (sample and test directions as factors) revealed a significant main effect of both sample direction ($F(1,8) = 6.43, p = 0.018$, one-tailed) and test direction ($F(1,8) = 9.61, p < 0.01$, one-tailed) on pulse identification. The interaction effect between the two factors was not significant ($F(1,8) = 1.70, p = 0.23$).

The average difference in performance between sample-same and sample-opposite trials (pooled across test directions) was 12%, an estimate of the effect of FBWM on pulse identification. This magnitude was similar to the difference in performance between sample-same and sample-opposite trials in Experiment 1 (11%). The average difference in performance between test-same and test-opposite trials (pooled across sample directions) was 14%, an estimate of the magnitude of the effect of FBA on pulse identification. Again, this magnitude was similar to the difference in performance between test-same and test-opposite trials in Experiment 2 (13%). The average

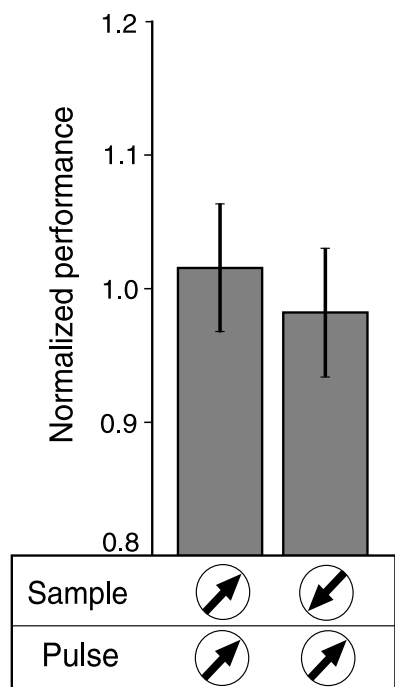


Figure 10. Results from Control 1. Mean normalized performance across all subjects in sample-same and sample-opposite trials of Experiment 2. Error bars indicate standard errors. The illustration depicts the relationship between the directions of the sample and the pulse in each condition.

co-occurring with the pulse. From these results, we concluded that maintaining a direction of motion in WM, as well as attending to a motion direction, can modulate motion perception. However, it could be argued that the observed effects were not necessarily due to the maintenance of the sample direction in WM or attending to the test, but by mere exposure to the sample or the test (e.g., sensory priming by the sample, or perceptual grouping of the test and the pulse). To rule out this possibility, we carried out two additional procedures, referred to as Control 1 and Control 2.

Control 1

In Experiment 2, we presented a sample RDP identical to the one in Experiments 1 and 3 (Figure 4b). However, this stimulus was not relevant for any of the tasks. This allowed us to test whether the direction of the sample influences pulse identification when subjects are exposed to it but do not maintain it in WM.

As described earlier, there were two types of trials in Experiment 2: test-same and test-opposite. Within each type, trials were randomly divided into: (a) those in which the sample and the pulse directions were the same (sample-same), and (b) those in which these directions were opposite (sample-opposite). Half of the trials were sample-same and half were sample-opposite. Performance

in the pulse identification task was measured as described in the Data analysis section of Experiment 1.

Across subjects, mean normalized performance was similar between sample-same and sample-opposite trials (Figure 10; $t(6) = 0.072$, $p = 0.47$, one-tailed paired-samples t -test). We conclude that the effect of the sample direction on pulse identification performance observed in Experiment 1 was not due to exposure to the sample per se, but rather to the maintenance of the sample direction in WM.

Control 2

In Experiments 2 and 3, subjects were better at identifying the direction of the pulse when it was the same as the one of the co-occurring test than when it was opposite. As proposed above, it can be argued that this effect might not be due to attention to the test direction but rather to mere exposure to the test during the presentation of the pulse. To discard this possibility, we performed an additional experiment. This experiment also served to corroborate that pulse identification performance was not affected by presentation of the sample itself, but rather by the maintenance of the sample direction in WM.

The procedure was identical to that of Experiment 3, except that subjects were instructed to perform the pulse

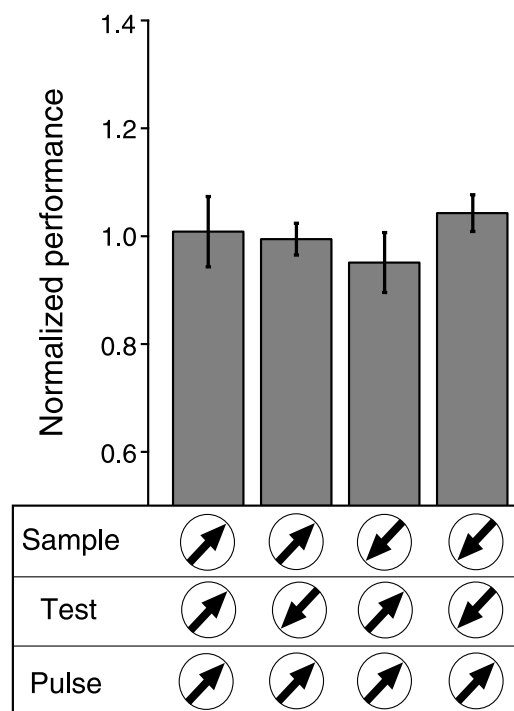


Figure 11. Results from Control 2. Normalized performance averaged across all subjects in each condition: sample-same/test-same, sample-same/test-opposite, sample-opposite/test-same, and sample-opposite/test-opposite. The illustration depicts the relationship between the directions of the sample, test, and pulse.

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