RAPID REPORT

The contradictory influence of velocity: representational momentum in the tactile modality

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¹Department of Psychology, University of Trier, Trier, Germany; ²Department of Psychology, University of Leipzig, Leipzig, Germany; ³Leibniz-Institut für Wissensmedien, Tübingen, Germany; and ⁴Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom

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Merz S, Deller J, Meyerhoff HS, Spence C, Frings C. The contradictory influence of velocity: representational momentum in the tactile modality. J Neurophysiol 121: 2358-2363, 2019. First published April 10, 2019; doi:10.1152/jn.00128.2019.-Representational momentum (RM) is the term used to describe a systematic mislocalization of dynamic stimuli, a forward shift; that is, an overestimation of the location of a stimulus along its anticipated trajectory. In the present study, we investigate the effect of velocity on tactile RM, because two distinct and contrasting predictions can be made, based on different theoretical accounts. According to classical accounts of RM, based on numerous visual and auditory RM studies, an increase of the forward shift with increasing target velocity is predicted. In contrast, theoretical accounts explaining spatiotemporal tactile illusions such as the tau or cutaneous rabbit effect predict a decrease of the forward shift with increasing target velocity. In three experiments reported here, a tactile experimental setup modeled on existing RM setups was implemented. Participants indicated the last location of a sequence of three tactile stimuli, which either did or did not imply motion in a consistent direction toward the elbow/wrist. Velocity was manipulated by changing the interstimulus interval as well as the duration of the stimuli. The results reveal that increasing target velocity led to a decrease and even a reversal of the forward shift, resulting in a backward shift. This result is consistent with predictions based on the evidence from tactile spatiotemporal illusions. The theoretical implications of these results for RM are discussed.

NEW & NOTEWORTHY This study tests two distinct predictions concerning the influence of velocity on the localization of dynamic tactile stimuli. We demonstrate for tactile stimuli that with increasing velocity, a misperception in the direction of anticipated motion (termed "representational momentum") turns into a misperception against the direction of motion. This result is in line with predictions based on tactile spatiotemporal illusions but challenges classical theoretical accounts of representational momentum based on evidence from vision and audition.

motion perception; representational momentum; spatiotemporal perception; tactile localization; velocity perception

INTRODUCTION

The localization of moving stimuli is undoubtedly important for the effective interaction with our surroundings. In our everyday life, we experience different moving objects (e.g., cars) and people. To navigate around them, and to avoid collisions, the accurate localization of these objects is essential. Interestingly, decades of visual research have revealed that any object that is seen to move in a predictable manner is typically not localized accurately, but is instead systematically misperceived along its anticipated trajectory (representational momentum, RM; Freyd and Finke 1984). More specifically, a systematic mislocalization of a moving object in the direction of anticipated motion, a forward shift, has been evidenced in many different studies (e.g., Freyd and Finke 1984, 1985; Hubbard and Bharucha 1988; for reviews, see Hubbard 2005, 2014). By now, this effect has been demonstrated in the visual (e.g., Freyd and Finke 1984, 1985) and auditory modalities (e.g., Feinkohl et al. 2014; Getzmann and Lewald 2007) and, more recently, in the tactile modality (Merz et al. 2019), as well.

In studies of visual and auditory RM, the velocity of the target turns out to be "one of the most robust influences" (Hubbard 2005, p. 828; Hubbard 2014) on the forward shift. The momentum of an object is defined as the product of its mass and velocity (Hubbard 2010), and with greater velocity, the momentum (and therefore the expected forward shift) increases (see Fig. 1*A*). This effect is predicted by all theories of RM (for an overview, see Hubbard 2010) and has been documented in numerous studies (e.g., De Sá Teixeira et al. 2013; Freyd and Finke 1985; Hubbard and Bharucha 1988; for reviews, see Hubbard 2005, 2014). However, based on previous studies on tactile spatiotemporal perception, it seems unlikely that this pattern of results will necessarily generalize to the tactile modality.

Evidence from the tau effect (i.e., shorter temporal intervals between two stimuli reduces the perceived spatial distance between them; Helson 1930) or the cutaneous rabbit illusion (whereby illusory tactile percepts are localized as occurring in between two spatially separate tactile stimulations; i.e., Geldard and Sherrick 1972) both suggest a different pattern of results. That is, with increasing velocity, the forward shift is expected to diminish and might even reverse to become a backward shift (that is, systematic misperception against the direction of motion; see Fig. 1*A*). This prediction has been corroborated by the perceptual length contraction account (Goldreich 2007; Goldreich and Tong 2013; Tong et al. 2016).

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Fig. 1. Predictions, experimental setup, and results of *experiments 1* and 2*a*. A: illustrative predictions of the influence of velocity on tactile representational momentum (RM) based on either visual and auditory RM studies (solid line) or tactile spatiotemporal illusions (dashed line). B: depiction of the experimental setup and its key characteristics illustrating a schematic view of the forearm with the 7 tactors (numbers indicate distance from center in cm; shaded circles indicate 2 tactors that were attached to the arm bandage but never used during the experiment). C: shift scores as a function of interstimulus interval (ISI) and stimulus duration of *experiments 1* and 2*a*. Shaded lines represent individual participant data; circles represent the means.

According to this account, perception reflects the product of the prior expectation concerning the stimulus and the likelihood of the sensory information. The authors argue that since most experiences with tactile stimuli are either static or slowly moving (e.g., feeling clothes moving over the skin), observers develop an expectation for slow velocities in the tactile modality. When fast velocities are present, this expectation is violated and the stimulus is perceived as being shorter than its actual length. Because presentation time is constant, the velocity of the stimulus is subsequently perceived to be slower than it actually was. Accordingly, the implied forward shift is expected to decrease in size or perhaps might even turn into a backward shift with increasing velocity in the tactile modality.

Overview

We set out to investigate these contrasting predictions by conducting a task that was designed to investigate tactile RM (see Merz et al. 2019), by presenting static tactile vibrations to different locations along the participant's forearm. In each trial, three discrete vibrotactile stimuli were delivered to three of five different locations, arranged in a straight line from the wrist to the elbow, on the left forearm. The vibrations were either presented from adjacent stimulators in a consistent direction, therefore "implying" the motion of a stimulus in a single direction (motion stimulus; for a review of the neural processing of tactile motion stimuli, see Pei and Bensmaia 2014), or else were located at three random locations along the forearm (control stimulus). The forward shift or motion displacement ("M displacement;" Hubbard 2005) is assessed as the difference between the perceived location of the motion and the control stimulus.

In *experiment 1*, the duration and the interstimulus interval (ISI) of the vibrotactile stimuli were manipulated separately to present varying velocities on the forearm. To ensure that changes in the perceived (forward) shift stem from the manipulation of the velocity, not from changes in the quality of the percept of the motion trajectory (see Cholewiak and Collins 2000), participants rated the perceived continuity of the stimulus sequence. Experiment 2a constitutes a replication of experiment 1 with a slightly reduced experimental design to replicate the findings of *experiment 1*. In *experiment 2b*, the control stimulus was omitted, because the mix of motion and control stimulus is not common in RM experiments in the visual and auditory modalities (e.g., see Freyd and Finke 1984). To foreshadow the results, the forward shift decreases and even reverses with increasing velocity, in line with the prediction based on the evidence from other spatiotemporal tactile illusions.

METHODS

Experiment 1

Participants. To elicit at least medium effect sizes ($dz \approx 0.6$) for an effect of velocity on the forward shift, we aimed for 32 participants in *experiment 1* ($\alpha < 0.05$; $1 - \beta > 0.95$; power analyses were run with G*Power 3.1.9.2; Faul et al. 2009). The final sample consisted of 32 students (17 women, 7 left-handed; 20-30 yr, mean age 24.38 yr) from the University of Trier. All of the participants reported normal or corrected-to-normal vision and no sensory impairment on their forearm, and all gave written informed consent before participation. The study was conducted in accordance with the research license of the University of Trier to conduct human studies. Note that an additional ethics commission is only required in case of potentially harmful

content of a study (e.g., invasive methods, explicit material) and was therefore not required for the present study.

Design. The participants were tested in a $2 \times 2 \times 2 \times 2 \times 3$ design with the five within-participant factors of stimulus type (implied motion vs. control), direction (proximal vs. distal), duration (100 vs. 250 ms), ISI (100 vs. 250 ms), and location (central: 0 cm vs. outer: ± 3.5 cm vs. outermost: ± 7 cm). For the subjective rating, the participants were tested in a $2 \times 2 \times 2$ design with the within-participant factors of direction (proximal vs. distal), duration (100 vs. 250 ms), and ISI (100 vs. 250 ms).

Apparatus, stimuli, and procedure. A detailed description of the apparatus, stimuli, and procedure can be found in Merz et al. (2019; Experiment 2). With the help of an arm bandage, five tactors (model C-2, Engineering Acoustic; 3 cm in diameter, centrally located skin contactor of 0.76 cm) were used to present vibrotactile stimuli (~250 Hz, ~126-µm peak-to-peak amplitude) to the volar side of the left forearm (see Fig. 1B). Seven tactors (two more tactors were attached to increase uncertainty about the location of the vibrations) were attached in a straight line, one next to the other (3.5 cm intertactor spacing). A 250-mm ruler (0 mm at the wrist, 250 mm at the elbow) was attached to the top of the arm bandage. The participants wore earplugs (noise reduction: 29 dB) on top of which brown noise (simultaneously presented frequency distribution with higher intensities at lower frequencies) was presented over headphones (over-ear headphones: ~85 dB) to block the lower frequency sounds (~250 Hz) elicited by the vibrotactile stimulation.

Each trial started with the presentation of a visual plus sign for 400 ms. Thereafter, three vibrotactile stimuli were presented successively for a duration of 100 or 250 ms and at a varying ISI of 100 or 250 ms. Stimulus duration as well as ISI was not changed during trials, but rather between them. Following the offset of the third vibration, the participants indicated the location of the last vibration, the target vibration, by pointing with their right index finger toward the corresponding location on the ruler, which the experimenter then noted. For the subjective rating, participants judged the continuity (not velocity) of the implied motion trials on a visual analog scale, ranging from 0 (impression of separate vibrations/events at distinct places) to 100 (impression of one continuously moving vibration/event).

In half of the trials, the vibrotactile stimuli were presented adjacent to each other in a single consistent direction (implied motion stimulus). Therefore, these stimuli implied a motion from one tactor to the next along the participant's forearm. For each direction condition (proximal direction: toward the elbow; distal direction: toward the wrist), three target locations were used, that is, the central (0 cm), outer (\pm 3.5 cm), and outermost (\pm 7 cm) location; see Fig. 1*B*). In the other half of trials, the control trials, the locations of the vibrations' locations were selected randomly without replacement with the restriction that implied motion condition trials never occurred. Overall, the participants completed 8 practice trials (random selection) and 384 experimental trials: 2 (stimulus type) × 2 (direction) × 2 (duration) × 2 (ISI) × 3 (location) × 8 (repetitions). For the subjective rating, 32 implied motion trials at the outer target location were used: 2 (direction) × 2 (ISI) × 2 (duration) × 4 (repetitions).

Analysis. Sixty-five trials (0.53%) in which the experimenter could not reliably recognize the indicated location were excluded from the analysis. The control trials were averaged to calculate a control estimate for each of the five tactor locations. Analyses were computed with shifts (in mm) as the dependent variable. The shift is the difference between the location estimation of the implied motion and control conditions. A positive value indicates an estimation of the implied motion trials in the proximal (distal) direction as closer to the elbow (wrist) than the control trials (comparable to classic M displacement scores; Hubbard 2005). In a first step, the shift scores of the fastest (duration and ISI = 100 ms) and slowest (duration and ISI = 250 ms) were tested against 0 (Bonferroni-adjusted *P* values are reported). For the slowest condition, the existence of a forward shift is expected, based on visual and auditory RM studies (for reviews, see Hubbard 2005, 2014) as well as our previous tactile RM study (Merz et al. 2019). In a second step, we conducted a 2 (direction) \times 2 (duration) \times 2 (ISI) \times 3 (location) multivariate analysis of variance (MANOVA)¹ with Pillai's trace as criterion. For the sake of readability, only the effects of velocity, that is, the effect of ISI and duration on the forward shift, are reported in RESULTS; the full model for as well as all mean scores are reported in the APPENDIX. For the subjective rating scores, we conducted a 2 (direction) \times 2 (duration) \times 2 (ISI) MANOVA with Pillai's trace as criterion.

Experiments 2a and 2b

Participants. For *experiments 2a* and 2b, only the fastest and slowest velocities were used; therefore, the expected effect size was slightly increased (dz of 0.7). We aimed for at least 24 participants in *experiments 2a* and 2b. Due to an organizational error in *experiment 2a*, the final samples consisted of 28 (*experiment 2a*: 17 women, 4 left-handed; 18–42 yr, mean age 24.32 yr) and 24 students (*experiment 2b*: 17 women, 3 left-handed; 18–24 yr, mean age 20.21 yr) from the University of Trier. All of the participants reported normal or corrected-to-normal vision and no sensory impairment on the forearm, and all gave written informed consent before participation.

Design, apparatus, stimuli, and procedure. The design, apparatus, stimuli, and procedure were identical to those of experiment 1 with the following exceptions. Only two target locations (central vs. outer) and two velocities (duration and ISI: 100 vs. 250 ms) were used. Therefore, the two factors of ISI and duration from experiment 1 were combined into one factor of velocity. Additionally, in experiment 2b, no control trials were presented. Participants worked through 128 experimental trials in experiment 2a, 2 (stimulus type) \times 2 (direction) \times 2 (velocity) \times 2 (location) \times 8 (repetitions), and 80 experimental trials in experiment 2b, 2 (direction) \times 2 (velocity) \times 2 (location) \times 10 (repetitions).

Analysis. Sixteen trials (0.45%) in experiment 2a and two trials (0.10%) in experiment 2b were excluded from the analysis. As in experiment 1, the forward shift was computed and tested in experi*ment* 2a with a 2 (direction: proximal vs. distal) \times 2 (velocity: duration and ISI = 100 vs. 250 ms) \times 2 (location: central vs. outer) MANOVA with Pillai's trace as criterion. Once again, only the effect of velocity is reported in RESULTS. The full model is reported in the APPENDIX. For experiment 2b, the same $2 \times 2 \times 2$ MANOVA was conducted, but with the mean localization scores (possible range: 0-250 mm; high scores indicate a localization close to the elbow) as the dependent variable because the control trials were omitted in this experiment. Therefore, the critical effect is now the interaction between velocity and direction. We expected localizations closer to the elbow (i.e., higher mean localization scores) for slow rather than for fast velocities for proximal motion trials. For distal motion trials, the reversed pattern was expected. We expected localizations closer to the wrist (i.e., lower mean localization scores) for slow rather than for fast velocities for distal motion trials.

RESULTS

Experiment 1

Location estimation. A significant forward shift with a duration and ISI of 250 ms was found as expected [t(31) = 2.49, P = 0.018 (one-tailed), d = 0.44]. Increasing the velocity of the presented stimulus sequence led to a significant shift from a forward to a backward shift [t(31) = -4.88, P < 0.001, d = 0.86 (duration and ISI of 100 ms; see Fig. 1*C*)]. That is, the MANOVA revealed significant

¹ Note that all repeated-measures designs are inherently multivariate, and the MANOVA has the advantage that sphericity cannot influence the results (see e.g., Tabachnick et al. 2007).

main effects of duration $[F(1, 31) = 74.36, P < 0.001, \eta_p^2 = 0.706]$ as well as ISI $[F(1, 31) = 14.06, P = 0.001, \eta_p^2 = 0.31]$. Furthermore, an ordinal interaction between the two effects was evidenced $[F(1, 31) = 4.84, P = 0.035, \eta_p^2 = 0.135]$. As indicated in Fig. 1*C*, shortening the ISI had a weaker effect on the shift score at a duration of 250 ms (250 ms: +3.35 mm; 100 ms: +2.30 mm) than at a duration of 100 ms (250 ms: -3.24 mm; 100 ms: -7.49 mm). Overall, the results of *experiment 1* clearly highlight that with increasing velocity, the forward shift decreases and then reverses to become a backward shift.

Subjective rating. The subjective rating scores show a different pattern than the shift scores. A shorter ISI (100 ms: 42.71 vs. 250 ms: 34.49) indicated a more continuous impression of the stimulus sequence $[F(1, 31) = 24.25, P < 0.001, \eta_p^2 = 0.44]$. In contrast, a shorter duration (100 ms: 34.33 vs. 250 ms: 42.71) tended to indicate a less continuous impression but just failed to reach the level of statistical significance $[F(1, 31) = 3.61, P = 0.067, \eta_p^2 = 0.10]$. None of the other effects were significant [Fs < 2.11, Ps > 0.156]. Because the fastest (100-ms duration and ISI: 38.77) and slowest velocity conditions (250-ms duration and ISI: 39.09) were perceived to be similar [t(31) = -0.06, P = 0.952], we used these conditions in *experiments 2a* and 2b.

Experiments 2a and 2b

Experiment 2a. Comparable to *experiment 1*, a backward shift for the fastest velocity [t(27) = -4.82, P < 0.001, d = 0.91] was found (Fig. 1*C*). The forward shift for the slowest velocity was not significant [t(27) = 1.74, P = 0.094 (one-tailed), d = 0.33].² Additionally, the MANOVA revealed a significant main effect of velocity $[F(1, 27) = 49.84, P < 0.001, \eta_p^2 = 0.649]$.

Experiment 2b. The MANOVA revealed a significant interaction between direction and velocity $[F(1, 23) = 6.25, P = 0.020, \eta_p^2 = 0.214]$. This pattern of results is consistent with those reported in *experiments 1* and *2a*; that is, a slow-motion stimulus is perceived further along its motion trajectory as compared with a fast-moving stimulus. More specifically, the end point of a slow motion toward the elbow (proximal direction) is perceived closer to the elbow than a fast motion [t(23) = -3.73, P = 0.002, dz = 0.73 (see Fig. 2)]. This pattern was reversed for a motion toward the wrist (distal direction) descriptively, although not statistically [t(23) = 1.20, P = 0.482, dz = 0.25].

DISCUSSION

We set out to investigate the contradictory predictions concerning the influence of velocity on tactile representational momentum. Across three experiments, we used the same timing parameters, a duration as well as an ISI of 250 ms, which we used in our previous study (Merz et al. 2019) and which are typical for implied motion stimuli in the RM literature (e.g., Freyd and Finke 1984; for reviews, see Hubbard 2005, 2014). We were able to replicate the existence of the forward shift



Fig. 2. Localization scores of *experiment 2b* as a function of direction (proximal or distal) and velocity (100 or 250 ms). Higher scores indicate a localization closer to the elbow; lower scores indicate a localization closer to the wrist. Shaded lines represent individual participant data; circles represent the means.

with these timing parameter in our experiments. Based on this reference condition, we decreased the duration as well as the ISI to increase the implied velocity of stimulation, whereby we identified a systematic pattern of results. That is, with increasing velocity, the forward shift of tactile stimulation decreased and then reversed to become a backward shift.

To investigate the effect of velocity on tactile RM, we used an implied motion sequence, comprising three stimulations, similar to the classical RM studies of Freyd and Finke (1984, 1985). In *experiment 1*, we further asked participants about their perception of the different velocity conditions. Although the different velocity conditions were differently perceived (a shorter duration is perceived as less continuous), the pattern does not match the localization pattern. In fact, the fastest and slowest velocity patterns were perceived similarly but showed a clear difference in their localization estimations. Additionally, in experiment 2b, we omitted the control condition, because the mixed presentation of control and implied motion stimuli is not common for studies of RM (e.g., Freyd and Finke 1984, 1985). Still, the pattern of results stayed the same, a slow-moving stimulus was perceived further along its motion trajectory compared with a fast-moving stimulus. Interestingly, evidence from related studies that have investigated the tactile localization of continuously moving tactile stimuli (i.e., drawing a continuous line on the forearm), not implied motion stimuli as in this study, indicate a similar pattern of results (e.g., Macauda et al. 2018; Nguyen et al. 2016; Whitsel et al. 1986).

The influence of velocity in the present study is in line with the prediction based on tactile spatiotemporal illusions and the perceptual length contraction account (Goldreich 2007; Goldreich and Tong 2013; Tong et al. 2016) but would appear to stand in contrast to the existing RM literature from the visual and auditory modalities (see Hubbard 2005, 2014). On the basis of these results, should the conclusion be drawn that (end point) localization in the tactile modality is functionally different than in the visual and auditory modalities? That is, is the tactile modality influenced by a slow velocity prior, and the visual and auditory modalities by the momentum of the object? Such an extreme conclusion is perhaps unwarranted, since the

² Comparing the forward shift between *experiments 1* and 2*a* for the slowest velocity condition revealed an overall significant forward shift [t(59) = 3.03, P = 0.004, d = 0.39] and no difference between the experiments [t(58) = 0.50, P = 0.622], indicating the existence of the forward shift across both experiments.

basic idea of the slow velocity prior was originally introduced on the basis of studies conducted with visual stimuli (Stocker and Simoncelli 2006; Weiss et al. 2002). Furthermore, the existence of a pure tactile forward shift would not be predicted by the perceptual length contraction account. Therefore, the present results suggest that at least two biases, a motion (which elicits the forward shift at slow velocities) and a slow velocity bias (which elicits the reversal of the forward to a backward shift), influence the estimation in all modalities but that the impact of these biases is dependent on variables that have yet to be worked out.³ The modalities differ in their spatial resolution, so perhaps spatial localization acuity modulates the impact of these biases and is the driving factor underlining the differing results in the different modalities.

The present study is in line with the growing interest in tactile and multimodal systems to present meaningful and helpful information (e.g., to alert car drivers of potentially dangerous situations; see Gallace and Spence 2014; Meng and Spence 2015). In addition to the interest in a pure warning function, recent interest has shifted toward presenting meaningful information to the driver (Brewster and Brown 2004; Meng and Spence 2015; e.g., orientation information or the location of possible dangerous situations/objects via the location of a stimulus). Therefore, this line of research concerning

³ The present results further show a significant difference in the magnitude of the forward/backward shift between the directions of the motion. That is, a moving stimulus toward the elbow elicits stronger forward shifts/weaker backward shifts than a moving stimulus toward the wrist (for the data as well as statistical analyses, see the APPENDIX). For a detailed discussion of this effect, please refer to our previous paper (Merz et al. 2019), where we report and discuss in detail these directional differences for the first time. No robust interactions between direction and velocity were evidenced in our data.

the localization of dynamic stimuli in the different spatial modalities will be useful to improve the design of future information systems.

APPENDIX

Table A1 shows the data of *experiments 1, 2a*, and 2b as a function of target location (central, outer, or outermost), direction (proximal or distal), ISI (100 or 250 ms), stimulus duration (100 or 250 ms), and condition (implied motion or control). Higher values indicate localization closer to the elbow/in the proximal direction (location estimation) or a higher perceived continuity (subjective rating). The shift score indicates the difference between the implied motion and control trials. Positive shift scores indicate a forward shift; negative shift scores indicate a backward shift.

In Table A2, the full MANOVA model in *experiments 1, 2a*, and 2b is presented. For *experiment 1*, the shift scores were submitted to a location (central vs. outer vs. outermost) × direction (proximal vs. distal) × stimulus duration (100 vs. 250 ms) × ISI (100 vs. 250 ms) MANOVA with Pillai's trace as the criterion. For *experiments 2a* and 2b, a location (central vs. outer) × direction (proximal vs. distal) × velocity (duration and ISI = 100 vs. 250 ms) MANOVA with Pillai's trace as the criterion was conducted. For *experiment 2a*, the shift scores were used as a dependent variable; for *experiment 2b*, the mean localization scores were used.

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Table A1. Mean location estimations, shift scores, and subjective rating scores for experiments 1, 2a, and 2b

	ISI, ms	Variable	Central		Outer		Outermost	
Duration, ms			Proximal	Distal	Proximal	Distal	Proximal	Distal
			Exp	periment 1: localize	ution score			
		Control	127.85 (24.23)	127.85 (24.23)	159.53 (17.73)	101.77 (31.27)	190.42 (16.75)	68.60 (38.68)
250	250	Implied motion	136.20 (22.88)	131.12 (31.75)	165.72 (19.61)	100.77 (35.04)	194.83 (16.62)	65.16 (34.88)
		Shift score	8.35 (16.92)	-3.27(17.24)	6.20 (11.02)	0.99 (11.65)	4.41 (10.05)	3.44 (8.85)
250	100	Implied motion	132.81 (22.82)	128.40 (31.03)	163.01 (20.89)	100.05 (33.05)	192.94 (19.79)	66.97 (38.69)
		Shift score	4.97 (16.37)	-0.55(17.71)	3.49 (14.31)	1.72 (12.14)	2.53 (8.59)	1.64 (8.55)
100	250	Implied motion	128.45 (21.70)	135.45 (28.93)	158.36 (20.40)	108.82 (33.36)	189.28 (19.56)	71.70 (37.56)
		Shift score	0.60 (15.32)	-7.60(18.30)	-1.16(9.88)	-7.06(14.47)	-1.14(10.65)	3.09 (7.90)
100	100	Implied motion	119.09 (24.18)	136.61 (30.47)	150.14 (20.91)	110.06 (32.23)	186.17 (18.97)	74.11 (35.55)
		Shift score	-8.75 (15.54)	-8.76 (18.20)	-9.38 (13.24)	-8.30 (14.82)	-5.51 (10.44)	-4.25 (9.97)
			Ex	periment 1: subject	tive rating			
250	250	Rating score			38.05 (18.53)	40.12 (16.02)		
250	100	Rating score			44.06 (21.31)	48.60 (17.14)		
100	250	Rating score			29.03 (19.77)	30.76 (24.85)		
100	100	Rating score			37.91 (23.09)	39.62 (24.56)		
			Exp	periment 2a: localiz	ation score			
		Control	136.41 (30.54)	136.41 (30.54)	155.96 (25.46)	112.74 (36.58)		
250	250	Implied motion	140.67 (29.06)	138.89 (31.74)	162.90 (26.16)	111.86 (38.89)		
		Shift score	4.25 (12.45)	-2.48(12.54)	6.93 (9.61)	0.88 (9.68)		
100	100	Implied motion	129.71 (33.53)	146.67 (31.60)	147.30 (29.26)	121.27 (35.18)		
		Shift score	-6.70 (14.42)	-10.25 (10.79)	-8.66 (10.32)	-8.53 (10.50)		
			Exp	eriment 2b: localiz	ation score			
250	250	Implied motion	125.18 (28.84)	144.92 (26.82	153.01 (28.84)	113.66 (26.46)		
100	100	Implied motion	115.77 (27.33)	146.69 (28.24)	145.45 (25.60)	118.52 (27.10)		

Data are means (SD). ISI, interstimulus interval.

Table A2. Full MANOVA model in experiments 1, 2a, and 2b

Effect	F Value	P Value	$\eta_{ m p}^2$					
Experiment 1 depe	endent variable:	shift score						
DUR	74.34	< 0.001	0.706					
ISI	14.04	0.001	0.312					
DIR	5.47	0.026	0.150					
LOC	0.39	0.682	0.025					
$DUR \times ISI$	4.84	0.035	0.135					
$DUR \times DIR$	1.28	0.267	0.040					
$ISI \times DIR$	12.90	0.001	0.294					
$DUR \times LOC$	2.26	0.122	0.131					
$ISI \times LOC$	0.11	0.897	0.007					
$DIR \times LOC$	1.21	0.313	0.074					
$LOC \times DIR \times DUR$	1.19	0.319	0.073					
$LOC \times DIR \times ISI$	1.99	0.154	0.117					
$LOC \times DUR \times ISI$	1.55	0.229	0.094					
$\text{DIR} \times \text{DUR} \times \text{ISI}$	0.92	0.344	0.029					
$LOC \times DIR \times DUR \times ISI$	0.12	0.887	0.008					
Experiment 2a dep	endent variable	: shift score						
VEL	49.84	< 0.001	0.649					
DIR	6.98	0.014	0.205					
LOC	1.23	0.277	0.044					
$VEL \times DIR$	4.13	0.052	0.133					
$VEL \times LOC$	3.55	0.070	0.116					
$DIR \times LOC$	0.70	0.411	0.025					
$VEL \times DIR \times LOC$	0.81	0.377	0.029					
Experiment 2b dependent variable: mean localization score								
VEL	8.23	0.009	0.264					
DIR	0.69	0.413	0.029					
LOC	0.28	0.600	0.012					
$VEL \times DIR$	6.25	0.020	0.214					
$VEL \times LOC$	4.92	0.037	0.176					
$DIR \times LOC$	145.52	< 0.001	0.864					
$\underbrace{\text{VEL} \times \text{DIR} \times \text{LOC}}_{}$	0.15	0.706	0.006					

DIR, direction; DUR, duration; ISI, interstimulus interval; LOC, location; MANOVA, multivariate analysis of variance; VEL, velocity.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.M., J.D., H.S.M., C.S., and C.F. conceived and designed research; S.M. and J.D. performed experiments; S.M. analyzed data; S.M., J.D., H.S.M., C.S., and C.F. interpreted results of experiments; S.M. prepared figures; S.M. drafted manuscript; S.M., J.D., H.S.M., C.S., and C.F. edited and revised manuscript; S.M., J.D., H.S.M., C.S., and C.F. approved final version of manuscript.

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