

Introduction

Humans, as social creatures continually perceive others and predict what they think, feel, and, most importantly, what they will do. Recent approaches propose mental imagery as a key mechanism underlying the anticipation of the relevant future, conceptualizing it as a simulatory process that may rely on similar pre-activation mechanisms as other top-down prediction processes and act directly on perceptual structures (1).

Traditionally, visual imagery has been conceptualized as a top-down process, involving projections from fronto-parietal areas to visual areas, while visual perception has been framed as a purely bottom-up process arising from early visual to higher regions (2,3). However, an emerging body of research reported how top-down processes also play a fundamental role in perception. Accordingly, a series of studies showed how sensory information is actively shaped in light of prior predictions (4, 5, 6), and that these processes are neurally implemented through the reciprocal exchange of bottom-up and top-down influences throughout the neuronal hierarchy (7, 8). In line with the idea that imagery and perception rely on similar top-down prediction processes, several studies highlighted the influence of imagery on subsequent conscious perception, showing both inhibitory (9, 10,11) and facilitatory effects (12, 13, 14).

The present study tests, through a series of experiments, whether and how mental imagery shares with predictive processes the capacity of shaping visual perception in an action observation context. To test this hypothesis, we used a well-established experimental paradigm which demonstrated that expectations of an action, expressed as a verbal intention prior to the observed movement, shaped the viewers' low-level perception of the action's kinematic towards the expected trajectory (15, 16, 17) and adapted this into an imagery task.

In Experiment 1 participants were asked to observe videos of a hand moving and estimate its last seen position through a touch-screen response. Crucially, before the onset of each video, participants were asked to imagine either a reach or a withdrawal, cued by the different color of the object on the screen. To control that the perceptual bias was influenced by the preceding imagery task rather than the association of colors to actions, the same study was ran on a control group, wherein the imagery task was replaced by a counting task. Experiment 2 aims at investigating if the imagery-related bias in perception could also be observed in a psychophysical probe version of the same task, ruling out the contribution of motor and working memory aspects (18, 19) in the emergence of the perceptual distortion towards the imagined trajectory.

Objectives

- 1) To reveal a perceptual bias in the low-level perception of the action's kinematic associated to both the mental simulation and the expectation of an action.
- 2) To establish the perceptual nature of the observed effect

Methods

Fifty participants took part to Experiment 1) and were randomly assigned to either the Mental Imagery Group or Control Group.

In each trial (Fig.1) a static frame of the hand in a neutral position was shown. In the Mental Imagery group, participants were required to imagine the hand reaching if the object was green and withdrawing when the object was red. In the Control Group, participants were asked to count to 2 seconds from the appearance of the static frame. As soon as they had clearly visualised the action (Mental Imagery group) or finished counting (Control Group), participants provided a verbal response, which triggered the onset of the action sequence. This could either match or mismatch the previous mental image. Midway through the action, the hand suddenly disappeared. Participants estimated the last seen position of the hand by touching its last seen location on the touch screen. The analyses were conducted by subtracting the real final screen coordinate of the tip of the index finger from participants' selected screen coordinate on each trial. Each participants' average differences values were entered into a 2 (Group) X 2 (Action's direction) X 2 (Object's color) mixed measures ANOVA for the X- and Y- axes separately.

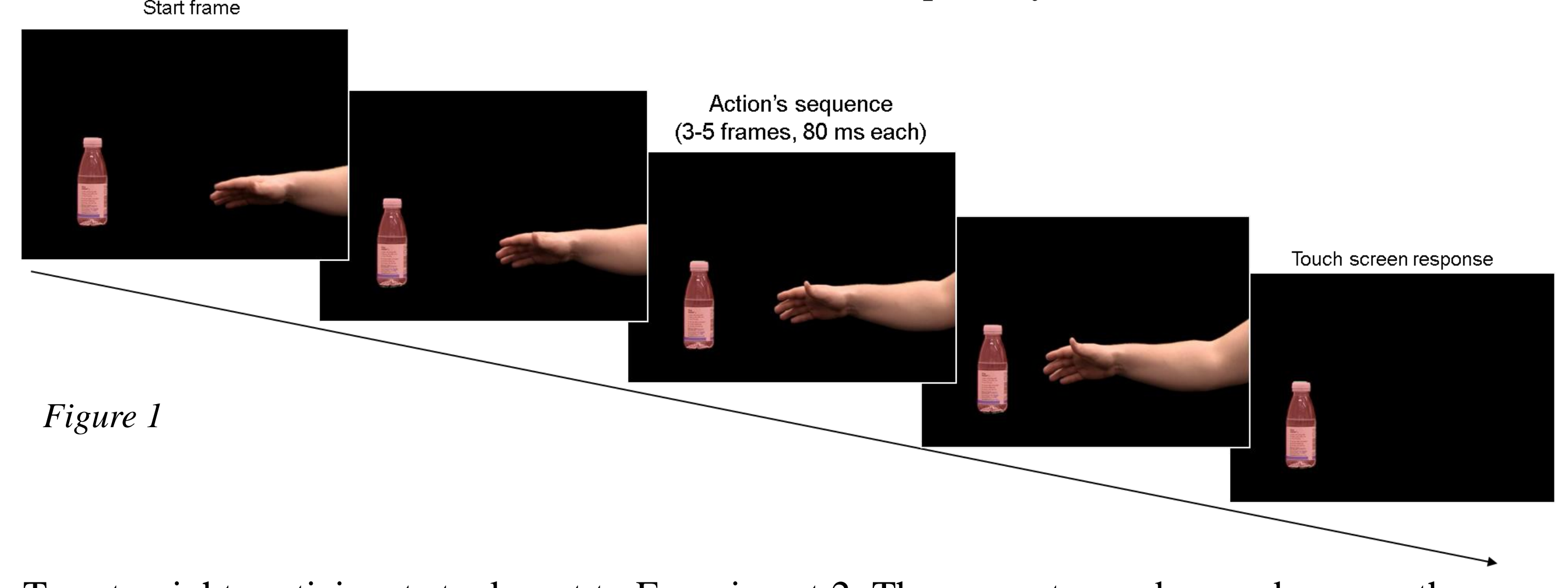


Figure 1

Twenty-eight participants took part to Experiment 2. The apparatus and procedure was the same as in Experiment 1. The only difference consisted in the absence of the touch-screen use for the recording of participants' behavioural response. Here, subjects judged the hand's disappearance point relative to probes presented after hand's offset (250 ms), that were either 1) identical to the hand's last seen position, 2) displaced forward along the trajectory ("+", nearer the object) 3) displaced backward ("-", away from the object). Participants pressed the spacebar if they thought the probe position was different from the hand's final position, and did not respond if they thought it was the same. Analyses were conducted by entering the frequency of individual "different" responses into a 2 (Action's direction) X 2 (Object's color) X 2 (Probe Direction) as repeated measures factors

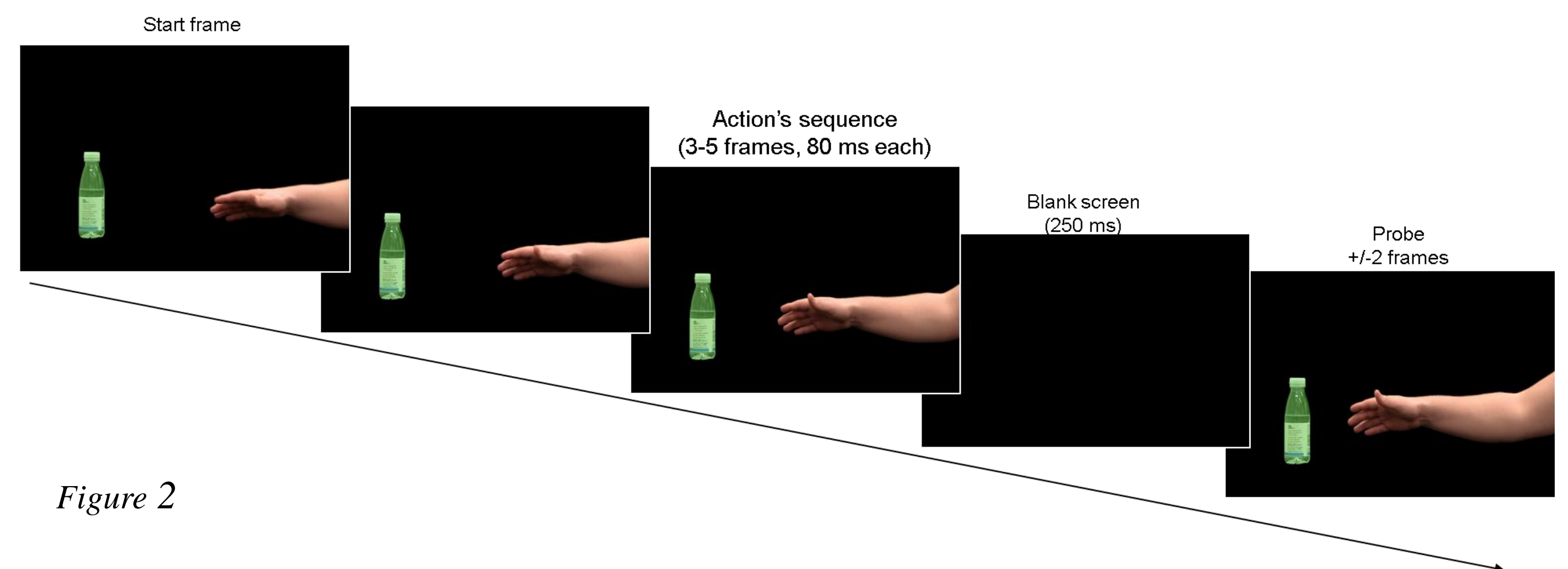
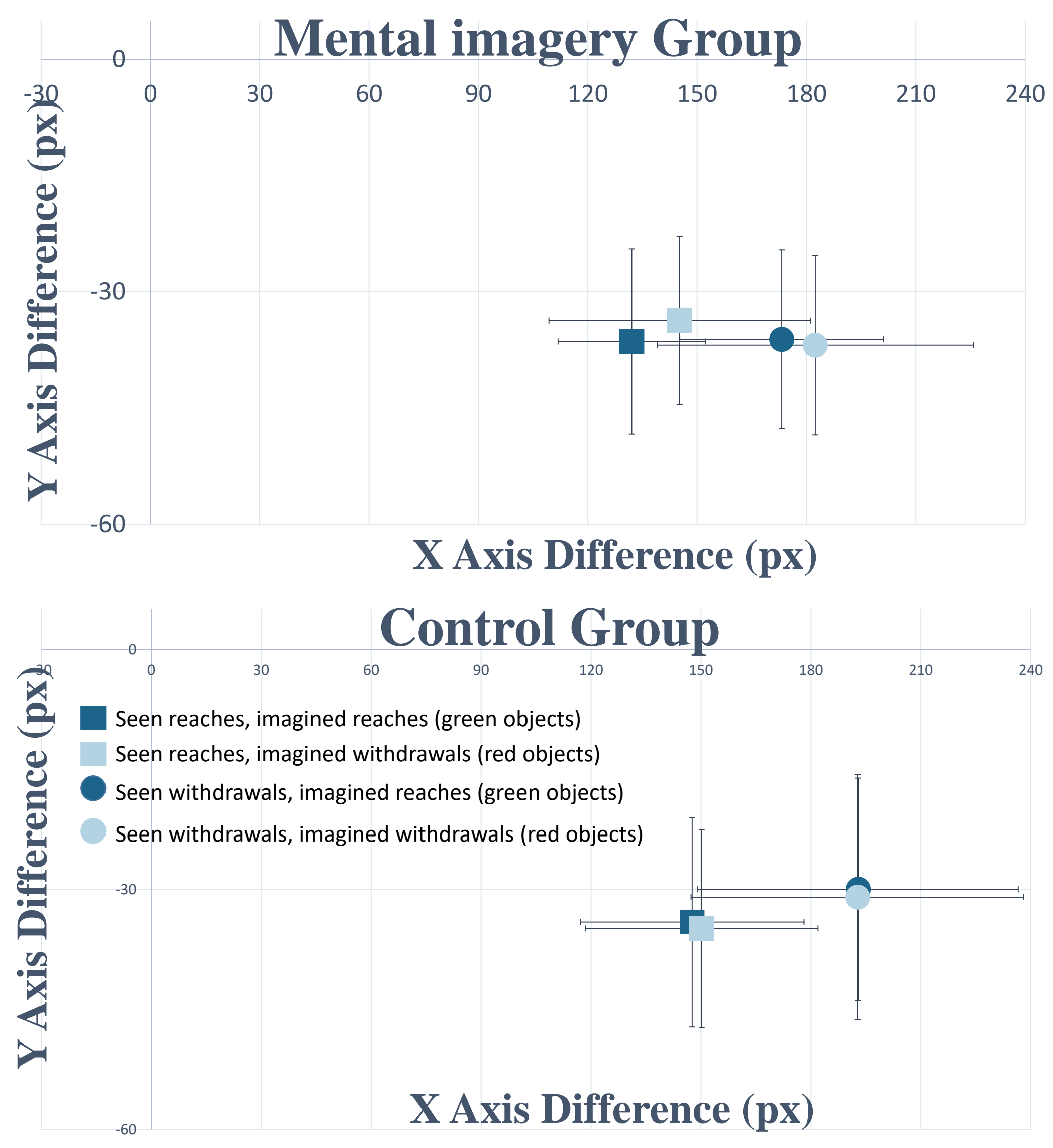


Figure 2

Results

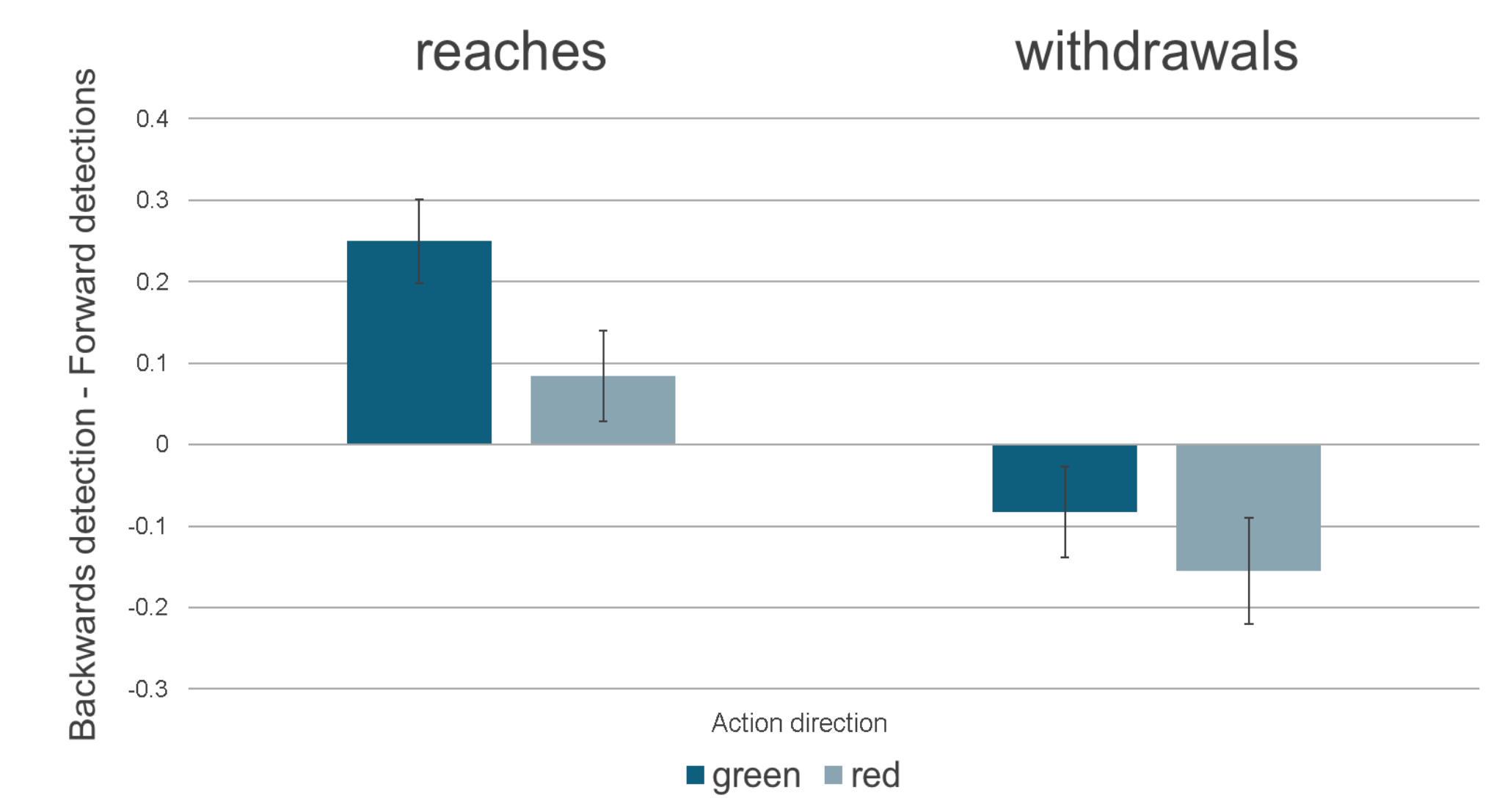
Reported hand disappearance points depending on which action was seen (reach/withdrawal) and which one was imagined



A main effect of Action ($F(1, 48) = 56.605, p < .001, \eta^2 = 0.541$), revealed a general predictive perceptual bias in the direction of motion, i.e. further leftward towards the object for reaches, than for withdrawals (i.e., representational momentum, (21)). It also revealed a main effect of Object Colour ($F(1, 48) = 52.486, p < .001, \eta^2 = 0.522$), showing that green objects (imagine a reach) generally produce a larger displacement leftwards towards the object than red objects (imagine a withdrawal). Importantly, this main effect was qualified by an interaction of Colour and Group, $F(1, 48) = 40.130, p < .001, \eta^2 = 0.455$, confirming that the perceptual bias was dramatically reduced in the Control Group. Indeed, step-down analyses revealed an effect of object's colour on the perceptual bias in the Mental Imagery group ($F(1, 23) = 16.053, p < .001, \eta^2 = 0.143$) but not the Control Group ($F(1, 23) = 0.025, p = 0.875, \eta^2 = 0.00$).

Figure 3. Values represent the difference between the selected disappearance point in pixels. An accurate response would produce a value of 0 on both axes. On the X-axis, positive values denote a rightward displacement and negative values a leftward displacement. Error bars represent SD.

Difference between the frequencies with which backward displaced probes were detected relative to forward probes.



As expected, the ANOVA showed a two-way interaction of Action and Probe direction ($F(1, 27) = 12.23, p < 0.002, \eta^2 = 0.312$), confirming that participants accepted more readily as "same" probes that were displaced in the direction of motion (i.e., representational momentum). Importantly, the ANOVA showed a two-way interaction of Object colour and Probe Direction ($F(1, 27) = 20.11, p < 0.001, \eta^2 = 0.427$), revealing that imagery of reaches (green objects) generally produced more "same" responses when forward probes were presented, and that imagery of withdrawals (red objects) was associated with more "same" responses when backward probes were presented.

Figure 4. Proportion of detected backwards minus forward probes. Positive values represent left perceptual shift and negative values represent right perceptual bias. Error bars represent SD

Conclusions

The results show, for the first time, evidence that imagery processes induce similar influences in how we visually perceive others' actions, as demonstrated before for explicit action predictions. In both Experiment 1 and Experiment 2, participants mis-identified the hand's last seen position further along the imagined trajectory than it actually was, by either actively reporting the disappearance point displaced further along the imagined trajectory (Experiment 1) or by misjudging – erroneously – as "same" probes displaced towards the visualized hand's trajectory (Experiment 2). This replication rules out that the effects emerge from perceptual changes to the action's representation in later working memory or motor control stages, and instead reveals a contribution of mental imagery to immediate perceptual processing. The evidence that the mental simulation of an action shapes its perceptual representation provide support for the assumption that imagery and perception rely on similar top-down prediction processes, and suggest that predictions might draw up on the same resources

References

1. Moulton, S. T., & Kosslyn, S. M. (2009). Imagining predictions: mental imagery as mental emulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1273-1280.
2. Denticto, D., Cheung, B. L., Chang, J. Y., Guokas, J., Boly, M., Tononi, G., & Van Veen, B. (2014). Reversal of cortical information flow during visual imagery as compared to visual perception. *Neuroimage*, 100, 237-243.
3. Mechelli, A., Price, C. J., Friston, K. J., & Ishai, A. (2004). Where bottom-up meets top-down: neuronal interactions during perception and imagery. *Cerebral cortex*, 14(11), 1256-1265.
4. Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature neuroscience*, 2(1), 79-87.
5. Sterzer, P., Frith, C., & Petrovic, P. (2008). Believing is seeing: expectations alter visual awareness. *Current Biology*, 18(16), R697-R698.
6. Lee, T. S., & Mumford, D. (2003). Hierarchical Bayesian inference in the visual cortex. *JOSA A*, 20(7), 1434-1448.
7. Bubic, A., Von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in human neuroscience*, 4, 25.
8. Den Ouden, H. E., Kok, P., & De Lange, F. P. (2012). How prediction errors shape perception, attention, and motivation. *Frontiers in psychology*, 3, 548.
9. Perky, C. W. (1910). An experimental study of imagination. *The American Journal of Psychology*, 21(3), 422-452.
10. Segal, S. J., & Fusella, V. (1970). Influence of imaged pictures and sounds on detection of visual and auditory signals. *Journal of experimental psychology*, 83(3p1), 458.
11. Arterberry, M., & Craver-Lemley, C. (2001). Imagery-induced interference on a visual detection task. *Spatial vision*, 14(2), 101-119.
12. Freyd, J. J., & Finke, R. A. (1984). Facilitation of length discrimination using real and imaged context frames. *The American journal of psychology*, 323-341.
13. Ishai, A., & Sagi, D. (1997). Visual imagery facilitates visual perception: Psychophysical evidence. *Journal of Cognitive Neuroscience*, 9(4), 476-489.
14. Pearson, J., Clifford, C. W., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology*, 18(13), 982-986.
15. Hudson, M., Nicholson, T., Ellis, R., & Bach, P. (2016). I see what you say: Prior knowledge of other's goals automatically biases the perception of their actions. *Cognition*, 146, 245-250.
16. Hudson, M., Nicholson, T., Simpson, W. A., Ellis, R., & Bach, P. (2016). One step ahead: The perceived kinematics of others' actions are biased toward expected goals. *Journal of Experimental Psychology: General*, 145(1), 1.
17. Hudson, M., Bach, P., & Nicholson, T. (2018). You said you would! The predictability of other's behavior from their intentions determines predictive biases in action perception. *Journal of experimental psychology: human perception and performance*, 44(2), 320.
18. Kerzel, D. (2003). Mental extrapolation of target position is strongest with weak motion signals and motor responses. *Vision Research*, 43(25), 2623-2635.
19. Müsseler, J., Stork, S., & Kerzel, D. (2008). Localizing the onset of moving stimuli by pointing or relative judgment: Variations in the size of the Fröhlich effect. *Vision Research*, 48(4), 611-617.
20. Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British journal of Psychology*, 64(1), 17-24.
21. Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10(1), 126.