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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
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Abstract

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People overestimate the final location of a moving object in the direction of the trajectory of that object. This distortion in visual perception, known as Representational Momentum (RM), aids in anticipating the behavior of moving objects. Because humans read from left to right, the effect might be stronger when objects move rightward. We tested RM in nonhuman primates to investigate if RM is shared by a nonhuman primate relative in the absence of reading directionality. Five rhesus macaques (*Macaca mulatta*) were trained to touch the final location of an object that moved horizontally across a touch screen. If the object moved leftward, the object stopped in one of two locations on the left side of the screen and vice versa if the object moved rightward. The monkeys were presented with two choice boxes, one around the position of object disappearance and one to the right or left, until they picked the choice box where the object disappeared ≥80% of the time for 2 consecutive sessions. In Experiment 1, we tested for RM by measuring if the subjects overestimated the final location of the white square using probes in which the choice stimuli intersected at the center of object disappearance. RM would manifest as a higher ratio for subjects to pick the choice square further along the trajectory of the object. In humans, increasing speeds can increase RM, so in Experiment 2, the object speed varied in order to investigate if velocity influenced RM in nonhuman primates. If RM exists in monkeys, then subjects will choose a location further along the trajectory of a moving object more often than a location prior to the point of disappearance. There was not an apparent RM effect in either experiment. In the future, we will test orangutans and gorillas to determine if RM exists in our closest evolutionary relatives.

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Introduction

The way in which organisms perceive the world is a constructive process, not just the result of passively received stimulation. People mentally anticipate the behavior of moving objects in a way that displaces the perceived final position of these objects in the direction of their motion (Hubbard, 2014). This is known as Representational Momentum (RM). RM is a phenomenon in visual perception in which objects moving along a path are thought to have moved further along that trajectory than they actually have (Freyd & Finke, 1984). The degree of forward displacement seen in RM is influenced by characteristics consistent with "momentum" such as velocity and size. For example, when an object is moving faster, RM increases (Halpern & Kelly, 1993; Hubbard, 2014; Perry, Smith, & Hockema, 2008). Researchers have theorized that this gives people an advantage by assisting them in pinpointing and anticipating the location of a moving target (Hubbard, 2005). Humans and rhesus macaques both have a middle temporal visual area (MT/V5) which is necessary for RM in humans (Rao et al., 2004). Also, people and monkeys both have a superior temporal sulcus (STS), which responds to motion and implied motion, and is inactive in older adults who do not show RM (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Piotrowski & Jakobson, 2011). Though people have proposed that the existence of RM in humans is evolutionarily advantageous, there has yet to be a RM study in nonhuman primates; our closest living evolutionary relatives.

Representational Momentum has been found across several types of tasks in humans. In same-different tasks a stimulus moves along a horizontal or rotational trajectory, around its own axis, and then disappears (Freyd & Finke, 1984). The next stimulus that appears is either in the same, to the left of, or to the right of the position of disappearance. Subjects are more likely to

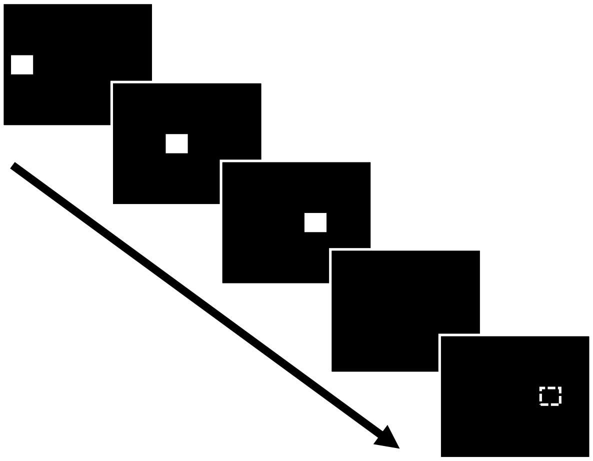

Figure 1: RM Location of Disappearance Task

In a typical Location of Disappearance RM task, a stimulus moves horizontally across the screen, stops, and disappears. After a delay of 125– 500ms, subjects indicate where they believe the final location of the target stimulus appeared on the screen. RM is inferred when subjects pick a location further along the trajectory of a stimulus. The white dotted line indicates a touch on the screen, and is not seen in the experiment.

incorrectly indicate that the probe stimulus is in the same position as where the target disappeared, when the probe position is further along the trajectory of the stimulus. In location of disappearance tasks, (**Figure 1**) subjects have to indicate the final location of a stimulus that disappeared along a horizontal trajectory. The motion of the target is either implied or continuous. There is no difference in RM between implied and continuous motion (Poljansek, 2002). Once the stimulus has vanished, participants are then asked to touch the position where the stimulus disappeared. In these disappearance tasks, subjects are also more likely to incorrectly indicate that the position of disappearance was further along the path of the stimulus (Hubbard, 2005).

Momentum is made up of both velocity and mass, so it is no surprise that these two elements can affect behaviors seen during the RM phenomenon. Velocity influences the amount of forward displacement seen in RM (Freyd & Finke, 1985; Hubbard, 1990). When infants see faster moving toy cars on a ramp apparatus with several occluders, they reach for the occluder further along the trajectory of the car (Perry et al., 2008). The effect of velocity on the degree of forward displacement in RM tasks is also evident in computerized tasks where targets moved horizontally (Hubbard, 2005). In the real world, faster moving objects are expected to be displaced more than slower moving objects within the same time frame, so the greater displacement seen in RM for faster moving objects is consistent with reality. Some experiments have manipulated perceived mass by changing the size of the target stimulus. The effect that size has on RM is less clear than the effect of velocity. Some experiments show that target size does not influence the degree of forward displacement (Hubbard, 2005), while other experiments have shown that when the size of the target increases, forward displacement increases (Hubbard, 2014). In reality, increasing mass will increase the momentum of an object, but experience shows that larger objects do not necessarily seem to move faster along a horizontal plane.

There are additional features of target stimuli that can impact the size of forward displacements seen in RM. Implied friction is one characteristic that has an inverse relationship with the degree of RM. Experimenters model “friction” in images by rotating objects in the opposite direction of their trajectory (backwards rotation). In a task in which subjects had to indicate the position where a forward rotating, backward rotating, or non-rotating target had vanished along a horizontal trajectory, implied friction blunted the effect of RM (Yamada, Kawabe, & Miura, 2010). The amount of forward displacement in trials with backward spinning stimuli was smaller than the displacement in the rest of the conditions.

Another feature that may affect RM is the direction that the target stimulus is moving. Most studies have shown that whether a target moves leftward or rightward, the degree of forward displacement is about the same (Hubbard, 2014). On the other hand, one study did show that the direction of movement does affect the size of the RM effect (Halpern & Kelly, 1993). In this study, when a stimulus moved to the right, there was a larger horizontal displacement between the actual position of stimulus disappearance and the judged position, compared to when a stimulus moved to the left. Therefore, according to the study, there is a greater "RM effect" for rightward moving objects than leftward. There is no reason in the physical world of objects for this to occur. Real objects do not move farther or faster in one direction than another. However, it is possible that reading directionality impacts the mental representation of moving objects (Halpern & Kelly, 1993). The subjects in this study were English-speaking students, so the bias in RM directionality may be due to the cultural influence of learning to read from left to right (Halpern & Kelly, 1993).

RM is also affected by the experience that participants have with the environment in which stimuli are presented as well as the experience subjects have with the trajectory of stimuli. Experienced drivers showed a greater RM effect in a same–different task with driving simulations than inexperienced drivers (Blattler, Ferrari, Didierjean, Elslande, & Marmeche, 2010). Participants viewed a driving scene, delay, and then a subsequent scene that was either the same as what the drivers saw when the scene stopped, a forward shift, or a backwards shift. Experienced drivers were more likely to choose the "same" choice for scenes that were actually forward shifts, and therefore "different" than inexperienced drivers. Similar results were shown in an aviation simulation. Pilots were compared to non-pilots in the same paradigm as above, but this time an aviation scene was used. Pilots showed the RM effect, but non-pilots did not (Blatter, Didierjean, Ferrari, & Marmeche, 2011). Thinking about experiences tied to an object can also affect the way people anticipate movement. Assigning participants to think of a target stimulus as a familiar mobile object increases forward displacement in the direction that the object moves in, in reality. In a vertical RM task, vertical displacement increased when the name assigned to an object (i.e. “Rocket”) exhibited vertical movements in the real world (Reed & Vinson, 1996). Experience shapes memories that people have with the environment and different objects, and as a result it also influences how people perceive movement.

Rhesus monkeys have experiences with moving objects as well. Rhesus macaques can also predict the future location of an occluded target stimulus (Filion, Washburn, & Gulledge, 1996). A computerized target prediction task was used in order to measure the ability of monkeys to locate the position of objects even when they are not seen. This ability is known as invisible displacement. This study shows that monkeys are capable of following the trajectory of moving objects, even when they are occluded. This is important because in order for RM to exist, subjects have to have a mental representation of unseen movement. In both human and rhesus monkeys there is a homologous brain region, the superior temporal sulcus (STS), that responds to motion and implied motion (Krekelberg et al., 2003; Piotrowski & Jakobson, 2011). There is another homologous brain region in primates (Sereno & Tootell, 2005) known as the middle temporal visual area (V5/MT) that is involved in motion detection and is necessary for RM to occur (Rao et al., 2004; C. Senior et al., 2000; Carl Senior, Ward, & David, 2002). RM has never been directly studied in nonhuman primates, but its existence could give insight into the evolutionary origin of RM as well as reveal more about how nonhuman primates respond to motion and implied motion. Additionally, because reading direction and language may affect RM in humans, studying RM in nonhuman primates could help to tease apart any influence these factors might have on the anticipation of movement.

The purpose of my study is to see if nonhuman primates exhibit RM in the absence of the cultural influences of reading direction and language. Subjects saw a moving target disappear at varying locations and had the choice of picking to the left or right of the position of disappearance. We also manipulated the momentum of the stimuli to see if RM behaved similarly in nonhuman primates by changing the velocity of these targets. If RM is similar in human and nonhuman primates, then velocity should influence the degree of the RM effect. We hypothesized that if Representational Momentum exists in nonhuman primates, then subjects will choose a location further along the horizontal trajectory of a moving stimulus more often than a location prior to the point of disappearance. If primates have a mental representation that is influenced by directionality, then subjects will show a greater RM effect in one directionality (leftward or rightward) than the other directionality. This would suggest that organizing motion spatially in one direction or the other is not just the byproduct of reading directionality. If primates have a mental representation that is influenced by velocity, then subjects will show a greater RM effect for faster moving objects than slower moving ones.

General Methods

Subjects

Subjects were 5 rhesus macaques (*Macaca mulatta*, mean age at start of testing = 7 years) housed at Yerkes Primate Research Center that had been raised by their biological mothers in a large social group until the age of approximately 2.5 years before moving to the laboratory. Monkeys were pair housed whenever possible and kept on a 12:12 light: dark cycle with light onset at 7:00 a.m. The monkeys were separated during testing. They received a full ration of food daily, and water was available ad libitum. Monkeys had previous experience with cognitive testing, but no experience with RM tasks.

Apparatus

Subjects were tested six days a week in their home cages, using portable testing rigs controlled by Visual Basic. Each rig was equipped with a 15 in. color LCD touch-screen (3M, St. Paul, MN) running at a resolution of 1024 ×768, generic stereo speakers, and two automatic food dispensers (Med Associates Inc., St. Albans, VT) that dispensed into food cups beneath the screen. Food rewards were nutritionally complete, banana or fruity flavored pellets (Bio-Serv, Frenchtown, NJ). One testing rig was attached to the front of each monkey's cage and remained there for 7 h, allowing the monkeys to work at their own pace during the day.

Training

To begin a trial, the subjects touched a green square twice (FR2) (**Figure 2**). A white square (100 x100 pixels) then appeared at either the left side of the screen (x, y: 5, 334) or the right side of the screen (920, 334) and moved smoothly along a horizontal trajectory at an average speed of 5 pixels per 15.5ms. All coordinates were measured from the upper left edge of each object. Stimuli starting on the right side of the screen traveled short and long distances leftward, stopping in 2 preset positions resulting in a Right Long non-test trial type and Right Short non-test trial type. Stimuli starting on the left side of the screen traveled short and long distances rightward, stopping in 2 preset positions resulting in a Left Long non-test trial type and Left Short non-test trial type (**Table 1 Figure 3**). After 100ms of being at the end locations, the white square disappeared. 500ms after the white square disappeared two purple choice boxes (150 x 150 pixels) appeared. One choice box appeared around the location of the disappeared square and the other appeared 220 pixels to the left or to the right of the first. This distance was measured from the center of each choice box. Subjects were reinforced for touching the choice box that appeared around the center of disappearance. Correct responses resulted in a food pellet, positive auditory feedback and an intertrial interval (ITI) of 3s. Incorrect trials were followed by no pellet, negative auditory feedback, and a time out during which the screen was black for 5s. Each of the non-test trial types were presented twice every 8 trials in a random order. There were 80 trials in a session for training. Once subjects reached 80% accuracy for two consecutive sessions they moved on to Experiment 1.

Experiment 1

Procedure

In Experiment 1, we tested whether subjects overestimated the location of white square disappearance in the direction of the trajectory of the object. Probe trials were similar to non-test trials except that the white square ended in different locations and purple choice boxes in probe trials overlapped at the center location of where the white stimulus disappeared (**Table 1 Figure 4**). There were two probe trial types, one in which the white square started on the right side of the screen and moved leftward, Right Probes, and the other in which the white square started on the left side of the screen and moved rightward, Left Probes. Probe trials were presented intermixed with non-test trials and occurred twice every 10 trials in a random order. There were 100 trials in a session in Experiment 1. Representational Momentum will be inferred if the subjects pick the purple square displayed further along the trajectory of the stimulus in probe trials more than 50% of the time. All probe trials were positively reinforced with both positive auditory feedback and pellet rewards no matter which choice monkeys made to minimize learning on test trials. Subjects completed 5 sessions.

Data Analysis

All proportion and accuracy data in this paper were arcsine-transformed before analysis to better approximate normality (Aron & Aron, 1999). We ran a one sample t–test to compare the accuracies of the final two training sessions to 50% chance to ensure the subjects learned the task. We also ran a one sample t-test in Experiment 1 to compare overall accuracies of non-test trials to the previous criterion of 80%. For probe trials, we were specifically interested in determining whether subjects touched the choice box further along the trajectory of the white square more often than the choice box closer to the start location. We performed a paired t–test comparing the percent subjects picked the left choice box in the Left Probe trials vs. the percent subjects picked left in Right Probes. RM is inferred if subjects pick left choice boxes more than right choice boxes in Right Probes and less in Left Probes; the t-test will show if picking the left choice box is different in the 2 trial types. The horizontal displacement data was analyzed by performing a one sample t-test comparing the distance between where the subjects touched in relation to the center of the location where the white square disappeared to zero.

Results and Discussion

The training accuracies at criterion were significantly different from chance, t (4) = 44.62, p <0.001 (M = 83.14, SD = 1.35, **Figure 5**). After reaching criterion two subjects ran additional sessions, due to a coding error. Only the data at and before these subjects reached criterion the first time were analyzed. Overall accuracies of non-test trials in Experiment 1 were not significantly different from the criterion of 80%, t (4) = -0.72, p = 0.509 (M = 77.60, SD = 6.94, **Table 2**). There was no clear Representational Momentum behavior in any of the 5 subjects nor in the aggregate data. If RM was present, then subjects would have picked the left choice box for leftward moving probes and the right choice box for rightward moving probes. There was no significant difference between the percent subjects picked the left choice box in Right Probes (M = 59, SD =31) and the percent subjects picked left choice boxes in Left Probes, (M = 48.20, SD = 24.80), t (4) = -0.81, p =0.462, RM cannot be inferred (**Figure 6**).

Additionally, there was no significant difference in horizontal displacement distances in pixels from 0, *t* (9) =2.26, *p* = 0.386 (*M* = -13.07, *SD* = 45.40, **Figure 7**).

In Experiment 1, there was no evidence of RM. This may be due to the speed of the white square stimulus. In humans, increasing the speed of the target stimulus increases the forward displacement seen in RM (Freyd & Finke, 1985). In Experiment 2, we manipulated the speed of the target stimulus to see if RM would be seen in our subjects when the target moved faster.

Experiment 2

We designed Experiment 2 in order to determine the impact of velocity on RM in nonhuman primates. In the previous experiment, RM was not seen in any of the subjects. Because RM is affected by velocity, we might be more likely to see an effect if we increased the velocity of the white square. This experiment addressed whether increasing the speed of the white square stimulus would reveal RM in nonhuman primates.

Procedure

Experiment 2 trials were identical to Experiment 1 except that the speed of the white square varied across sessions for both non-test and probe trial types. There were three white square speeds: slow, medium and fast. The slow speed was the same as Experiment 1 with a square movement of 5 pixels per 15.5ms (average), the medium speed squares moved 10 pixels per 15.5ms (average), and fast speed squares moved 20 pixels per 15.5 ms (average) (**Table 1**). The speeds varied by session: in session 1 all trials were slow, in session 2 all trials were medium, in session 3 all trials were fast, and in session 4 all trials were back down to slow. This pattern repeated until there were 15 total sessions, 5 at each speed.

Data Analysis

We performed a Repeated Measures analysis of variance (ANOVA) for the overall accuracies of non-test trial types across the 3 speeds. We also performed a Repeated Measures ANOVA on proportion left choice with probe direction as a factor across the 3 speeds. We performed a Repeated Measures ANOVA on the horizontal displacement of where the subjects touched in relation to the center of the location where the white square disappeared in pixels for both directions across the 3 speeds.

Results and Discussion

There was a significant effect of speed on non-test trial accuracy, F (2, 8) =8.66 p =0.011. A post hoc paired t-test showed that fast speed trial accuracies (M = 73.20, SD = 4.82) were significantly lower than the slow, t (4) = 2.80, p = 0.049, (M = 79.8, SD = 8.04) and medium speed trials, t (4) = 6.87, p = 0.002, (M = 79.4, SD = 6.27, **Figure 8**). Past human studies have shown that increasing the speed of a target would result in an increased RM (Freyd & Finke, 1985; Hubbard, 1990). However, in our subjects there was no significant difference between the percent subjects picked the left purple choice box for any of the speed conditions, F (2, 8) =0.2, p =0.823 or directions, F (1, 4) =0.33, p =0.595. There was no interaction between stimulus speed and direction, F (2, 8) =1.12, p =0.371 (**Figure 9**). There was also no significant difference between the horizontal displacement for any of the speeds, F (2, 8) = 0.09, p =0.915 or directions, F (1, 4) =0.678, p =0.456. There was no significant interaction between stimulus speed and direction, F (2, 8) =0.36, p =0.707 (**Figure 10**). The increase in square speed did not result in RM for any of the speed manipulations.

General Discussion

We did not find RM in either of the experiments. It is possible that RM does not exist in monkeys. Differences in neuroanatomy between human and nonhuman primates may explain why RM was not seen in this study. Although humans and macaques have a homologous brain region (STS) believed to be involved in RM, there may be additional anatomical variances that explain its absence in monkeys (Krekelberg et al., 2003). Human brains have highly lateralized functions including spatial cognition, but nonhuman primates do not seem to have the same spatial asymmetries (Oleksiak, Postma, Ham, Klink, & Wezel, 2011). RM is in fact larger when targets are seen in the left visual field, (Halpern & Kelly, 1993) which supports the impact of human brain laterality. Additionally, the right parietal lobe is more active during RM tasks than when the subject is idle (Amorim et al., 2000). These differences in anatomic asymmetry could be the reason for not seeing RM in our monkey subjects. Perhaps the expansion of lateralized spatial areas in humans drives RM.

It is also possible that the subjects did not show RM because they did not have real world experience with the objects that were used. As described previously in the aviation simulation experiment, non–pilots did not show RM (Blatter et al., 2011). This is believed to be due to the lack of experience non-pilots had with that particular environment. Perhaps if the subjects had more experience seeing white squares move all the way across a screen and then were tested on this experiment again, they would show RM. It is also possible that using real world objects that the monkeys have seen move around would be more likely to induce RM.

An additional explanation for the lack of Representational Momentum in these two experiments could be the way in which they were designed. The experiments start off with one object that moves and disappears. This object is then followed with two different static “choice” boxes with which the subjects must interact. RM experiments in humans are designed differently. In the RM experiments for people, any image used outside of the stimulus is a distractor and when a distractor task is not being used only one image is seen before subjects are tasked with picking the location of disappearance (Hubbard, 2005). If the characteristics of the stimulus being used in a human experiment (color, texture, shape, etc.) are slightly changed during a test, RM decreases. This research has also shown that RM can be completely eliminated if the characteristics of the target stimulus are dramatically changed (Freyd, 1987). Momentum seems to be attached to the moving object and its characteristics. In the current study, the stimulus object disappears and a new one appears, therefore momentum might not be transferred over. It is possible that RM was eliminated because of this design feature.

Visual spatial attention is necessary for RM to exist, so if attention is drawn away from the target, RM can be reduced (Kerzel, 2003a; Munger & Owens, 2004; Musseler, Stork, & Kerzel, 2002). Our experiment did not monitor the eye movements of the subjects, so we cannot report whether the subjects were always tracking the target. RM decreases in experiments with smoothly moving objects if subjects do not visually track the objects (Kerzel, 2003b). There is a possibility that subjects did not consistently track the target movement in this study. This explanation gives some insight on how the experimental design could be improved for future nonhuman primate testing. In the future, we could train monkeys on a same –different task in which visual tracking of target movement is unnecessary or a location of disappearance task in which the characteristics of the target stimuli seen by the subjects stays the same throughout each task.

The way in which subjects perceived the purple choice boxes could be an additional reason for not seeing RM. If the subjects perceived the purple choice boxes as boundaries, then the direction of displacement could have been affected. Although the purple boxes were not displayed while the target square was visible, they could have been associated with the boundaries of the white square due to training. In both experiments, target squares stopped in one of three preset positions on each side. These preset positions coincided with the purple box locations, so it is possible that the purple boxes could be viewed as boundaries of the target. RM can diminish or completely go away if an object is expected to stop when it approaches another object (Hubbard, 1994). It is also possible for the displacement of an object to go in the opposite direction of the object's trajectory (Hubbard & Motes, 2005). However, if this were the case the subjects would have underestimated for both probe directionalities.

In future studies, we would like to incorporate a spatial-numerical manipulation in our experimental design, in order to explore if primates represent magnitude in space. There is a numerical version of Representational Momentum known as Operational Momentum (OM). In this phenomenon, humans overestimate when summating and underestimate when subtracting (Hubbard, 2014). In Operational Momentum, the forward displacements are not in physical space, but rather along a mental number line (Dehaene, Bossini, & Giraux, 1993; McCrink, Dehaene, & Dehaene-Lambertz, 2007; McCrink & Wynn, 2009). This left to right number line is believed to be influenced by culture (Dehaene et al., 1993), but because infants also show OM there might be an innate predisposition to organize numbers in a rightward direction (McCrink & Wynn, 2009). Rhesus monkeys are able to add and subtract so it is plausible to test for OM in nonhuman primates (Cantlon & Brannon, 2007; McCrink et al., 2007; Sulkowski & Hauser, 2001). Monkeys displayed the ability to add in the same task used on humans (Cantlon & Brannon, 2007). This task used to test if monkeys are able to add can also be modified to measure OM. Because it is difficult to design a directly comparable task for both monkeys and humans, this paradigm that has already been tested in both species could be used to test for OM in nonhuman primates. In our current study, we had to employ choice boxes in order to ask where the square stimulus was last seen. In human studies, researchers can verbally instruct subjects to indicate where a stimulus was last seen without any potential distractors like choice boxes. A result of OM in our subjects would support our continued investigation of RM.

Though we did not see an RM effect in our subjects we will also test for RM in some of our even closer nonhuman primate relatives: gorillas (*Gorilla gorilla*) and orangutans (*Pongo abelii*). If RM is present in orangutans and gorillas in the same testing paradigm that did not reveal RM in rhesus macaques, then it could mean that RM is a great ape specialization. This research is the first step in exploring RM in nonhuman primates. Further tests designed to measure how nonhuman primates relate objects to space can help us understand the underlying mechanisms that cause phenomena such as RM in the absence of culture.

References

Amorim, M.-A., Lang, W., Lindinger, G., Mayer, D., Deecke, L., & AlainBerthoz. (2000). Modulation of Spatial Orientation Processing by Mental Imagery Instructions: A MEG Study of Representational Momentum *Journal of Cognitive Neuroscience, 12*(4), 569-582.

Aron, A., & Aron, E. (1999). *Statistics for psychology*. Upper Saddle River, NJ: Prentice Hall.

Blatter, C., Didierjean, A., Ferrari, V., & Marmeche, E. (2011). Representational Momentum in Aviation. *Journal of Experimental Psychology Human Perception and Performance, 37*(5), 1569-1577.

Blattler, C., Ferrari, V., Didierjean, A., Elslande, P. v., & Marmeche, E. (2010). Can expertise modulate representational momentum? *Visual Cognition, 18*(9), 1253-1273.

Cantlon, J. F., & Brannon, E. M. (2007). Basic math in monkeys and college students. *PLos Biol, 5*(12), 2912-2919.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The Mental Representation of Parity and Number Magnitude. *Journal of Experimental Psychology General, 122*(3), 371-396.

Filion, C. M., Washburn, D. A., & Gulledge, J. P. (1996). Can Monkeys (Macaca mulatta) Represent Invisible Displacement? . *American Psychological Association Inc., 110*(4), 386-395.

Freyd, J. J. (1987). Dynamic Mental Representations. *Psychological Review, 94*(4), 427-438.

Freyd, J. J., & Finke, R. A. (1984). Representational Momentum. *Journal of Experimental Psychology Learning, Memory, and Cognition, 10*(1), 126-132.

Freyd, J. J., & Finke, R. A. (1985). A velocity effect for representational momentum. *Bulletin of the Psychonomic Society, 23*(6), 443-446.

Halpern, A. R., & Kelly, M. H. (1993). Memory Biases in Left Versus Right Implied Motion. *Journal of Experimental Psychology Learning, Memory, and Cognition, 19*(2), 471-484.

Hubbard, T. L. (1990). Cognitive representation of linear motion: Possible direction and gravity effects in judged displacement. *Memory & Cognition, 18*(3), 299-309.

Hubbard, T. L. (1994). Judged displacement: A modular process? *American Journal of Psychology, 107*(3), 359-373.

Hubbard, T. L. (2005). Representation momentume and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin & Review, 12*(5), 822-851.

Hubbard, T. L. (2014). Forms of momentum across space: Representational, operational, and attentional. *Psychon Bull Rev, 21*, 1371-1403.

Hubbard, T. L., & Motes, M. A. (2005). An effect of context on whether memory for initial position exhibits a Frohlich effect of ran onset repulsion effect. *The Quaterly Journal of Experimental Psychology, 58A*(6), 961-979.

Kerzel, D. (2003a). Attention maintains mental extrapolation of target position: Irrelevant distractors eliminate forward displacement after implied motion. *Cognition, 88*, 109- 131.

Kerzel, D. (2003b). Mental extrapolation of target position is strongest with weak motion signals and motor responses. *Vision Research, 43*, 2623-2635.

Krekelberg, B., Dannenberg, S., Hoffmann, K.-P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature, 424*, 674- 677.

McCrink, K., Dehaene, S., & Dehaene-Lambertz, G. (2007). Moving along the number line: Operational momentum in nonsymbolic arithmetic. *Perception & Psychophysics, 69*(8), 1324- 1333.

McCrink, K., & Wynn, K. (2009). Operational momentum in large-number addition and subtraction by 9-month-olds. *Journal of Experimental Child Psychology*.

Munger, M. P., & Owens, T. R. (2004). Representational momentum and the flash-lag effect. *Visual Cognition, 11*(2), 81-103.

Musseler, J., Stork, S., & Kerzel, D. (2002). Comparing mislocalizations with moving stimuli: The Frohlich effect, the flash-lag, and representational momentum. *Visual Cognition, 9*(1/2), 120-138.

Oleksiak, A., Postma, A., Ham, I. J. M. v. d., Klink, P. C., & Wezel, R. J. A. v. (2011). A review of lateralization of spatial functioning in nonhuman primates. *Brain Research Reviews, 67*, 56-72.

Perry, L. K., Smith, L. B., & Hockema, S. A. (2008). Representational momentum and children's sensori-motor representations of objects. *Developmental Science, 11*(3), F17- F23.

Piotrowski, A. S., & Jakobson, L. S. (2011). Representational momentum in older adults *Brain and Cognition, 77*, 106-112.

Poljansek, A. (2002). The effect of motion acceleration on displacement of continuous and staricase motion in the frontoparallel plane. *Horizons of Psychology, 11*(2), 7-21.

Rao, H., Han, S., Jiang, Y., Xue, Y., Gu, H., Cui, Y., & Gao, D. (2004). Engagement of the prefrontal cortex in representational momentum: an fMRI study. *NeuroImage, 23*, 98-103.

Reed, C. L., & Vinson, N. G. (1996). Conceptual Effects on Representational Momentum. *Journal of Experimental Psychology Human Perception and Performance, 22*(4), 839-850.

Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., & David, A. S. (2000). The functional neuroanatomy of impicit-motion perception or 'representational momentum'. *Current Biology, 10*, 16-22.

Senior, C., Ward, J., & David, A. S. (2002). Representational momentum and the brain: An investigation into the functional necessity of V5/MT. *Visual Cognition, 9*(1/2), 81-92.

Sereno, M. I., & Tootell, R. B. (2005). From monkeys to humans: what do we now know about brain homologies. *Current Opinion in Neurobiology, 15*, 135-144.

Sulkowski, G. M., & Hauser, M. D. (2001). Can rhesus monkeys spontaneously subtract? *Cognition, 79*, 239-262.

Yamada, Y., Kawabe, T., & Miura, K. (2010). Representation momentum modulated by object spin. *The Japanese Journal of Psychonomic Science, 28*(212-220).

Figures

Trial types	Slow/ Training Speed	Medium Speed	Fast Speed
Right Short	*350*	*350*	*340*
Right Long	*130*	*130*	*120*
Left Short	*575*	*575*	*585*
Left Long	*795*	*795*	*805*
Right Probe	**240**	**240**	**240**
Left Probe	**685**	**685**	**685**

Table 1: **The X- Coordinates of the Left Edge of the White Square End Locations across all Trial Types and Speeds**

Probe trial type end locations remained consistent across all trial types. In the fast moving non-test trial types, end locations were shifted by 10 pixels in order for the distance traveled to remain divisible by 20. *Italic* end locations correspond to non-test trial types, and **bold** end locations correspond to probe trial types.

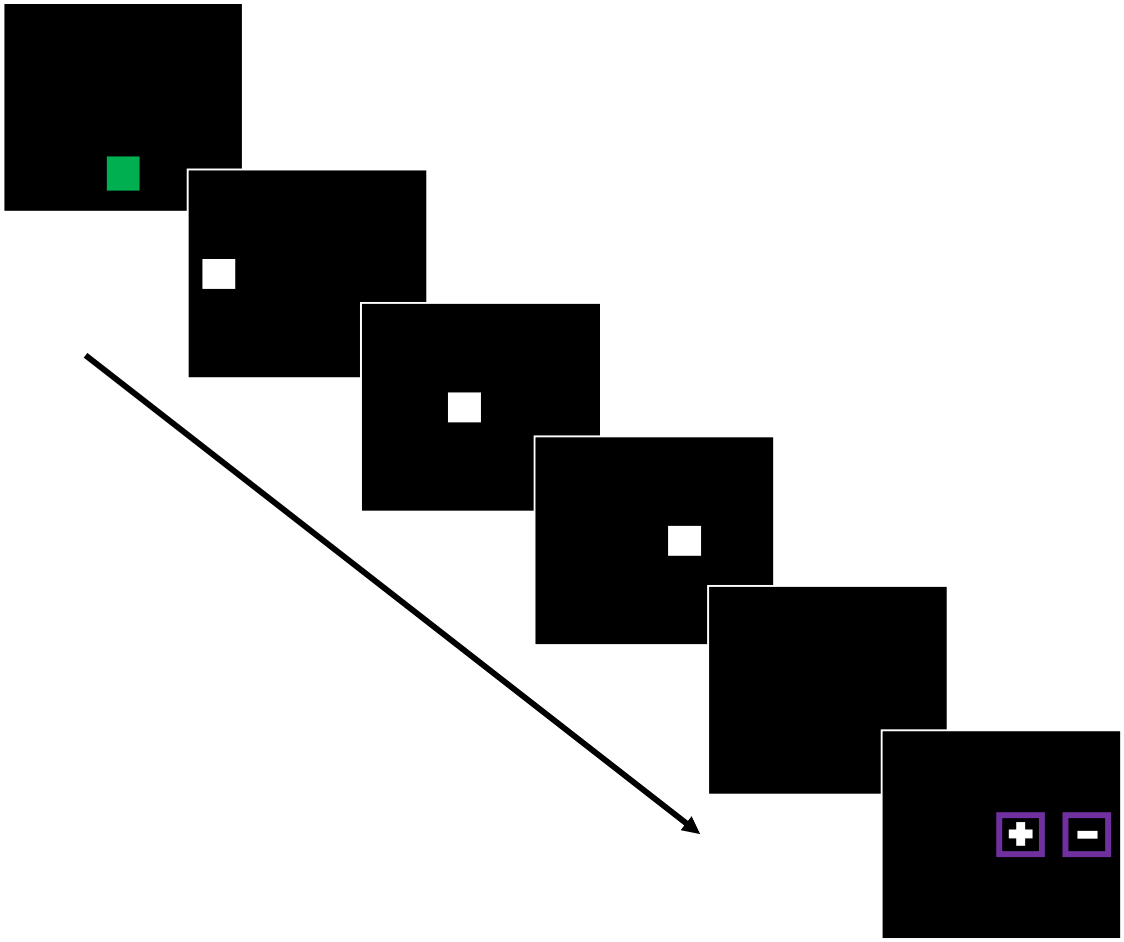

Figure 2: General Procedure

Subjects touched the green square twice to begin a trial. A white square appeared at either end of the screen and smoothly moved leftward or rightward. Once the square reached its designated end location, it disappeared. After a 500ms delay two purple choice boxes appeared, one around the center of white square disappearance (+) and the other either to the left or right (-). The (+) and (-) were not visible to the subjects.

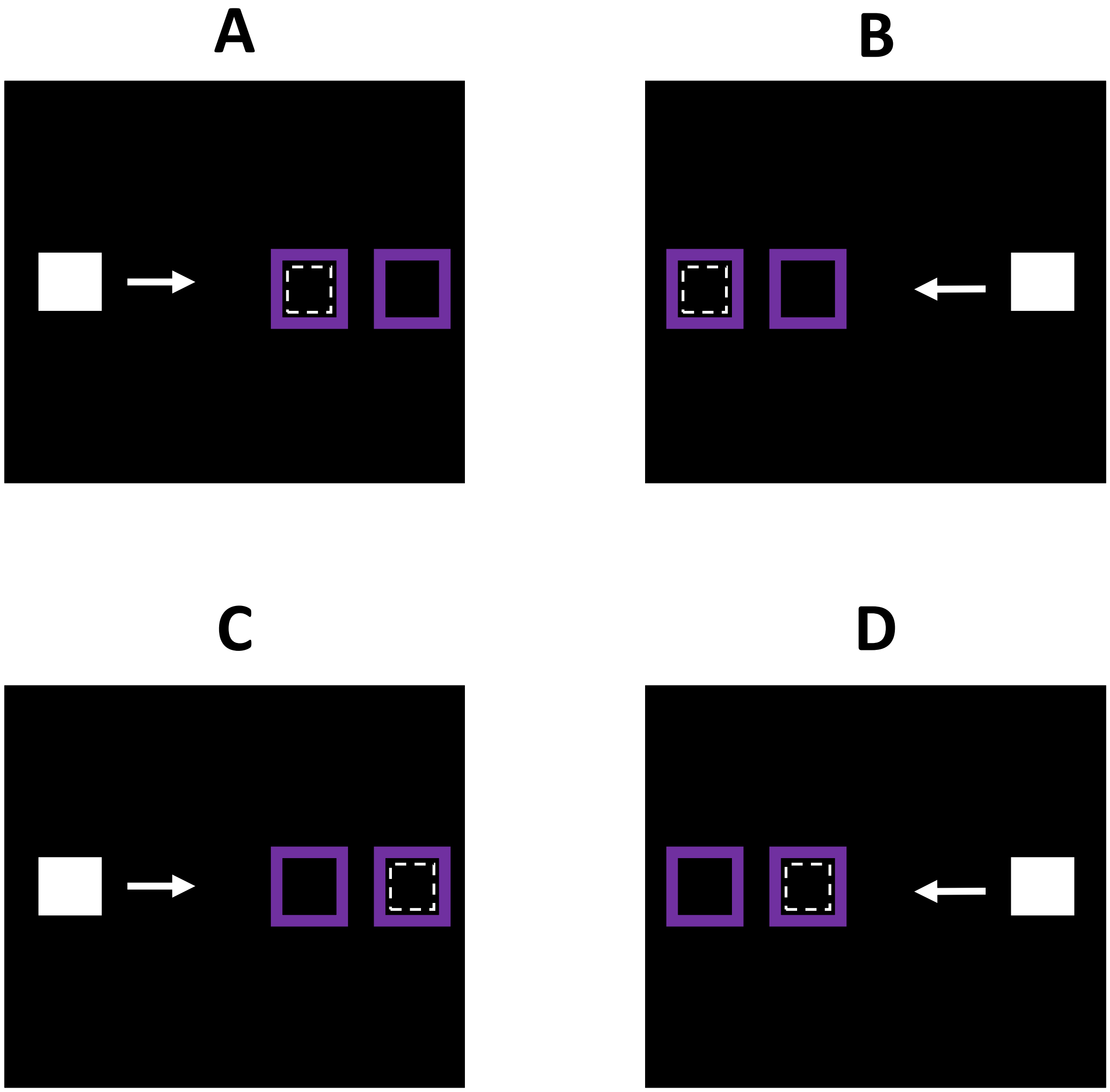

Figure 3: Non-Test Trial Types

All of the possible final positions of the white squares and purple choice boxes for non-test trial types. The white dotted line represents the location where the white moving stimulus stopped.

(**A**) Left Short (**B**) Right Long (**C**) Left Long (**D**) Right Short

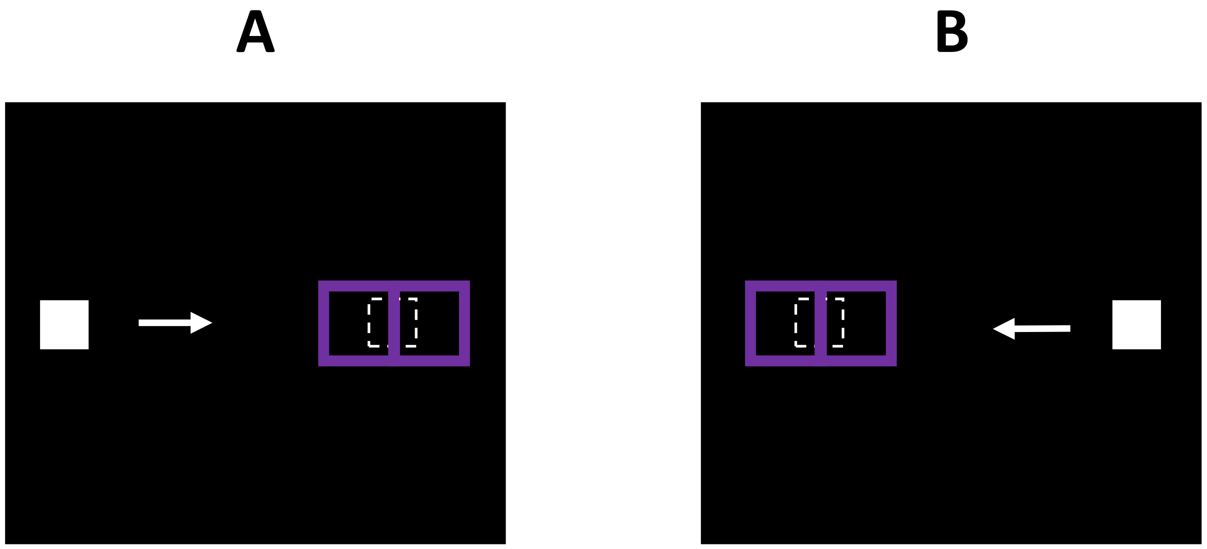

Figure 4: Probe Trial Types

Possible final positions of the white squares and purple choice boxes for probe trials. The two purple choice boxes fused around the center location of where the white square disappeared. The white square stopped in new end locations directly in between where the white square stopped in short and long non-test trial types. The white dotted line represents the location where the white moving stimulus stopped.

(**A**) Left Probe (**B**) Right Probe

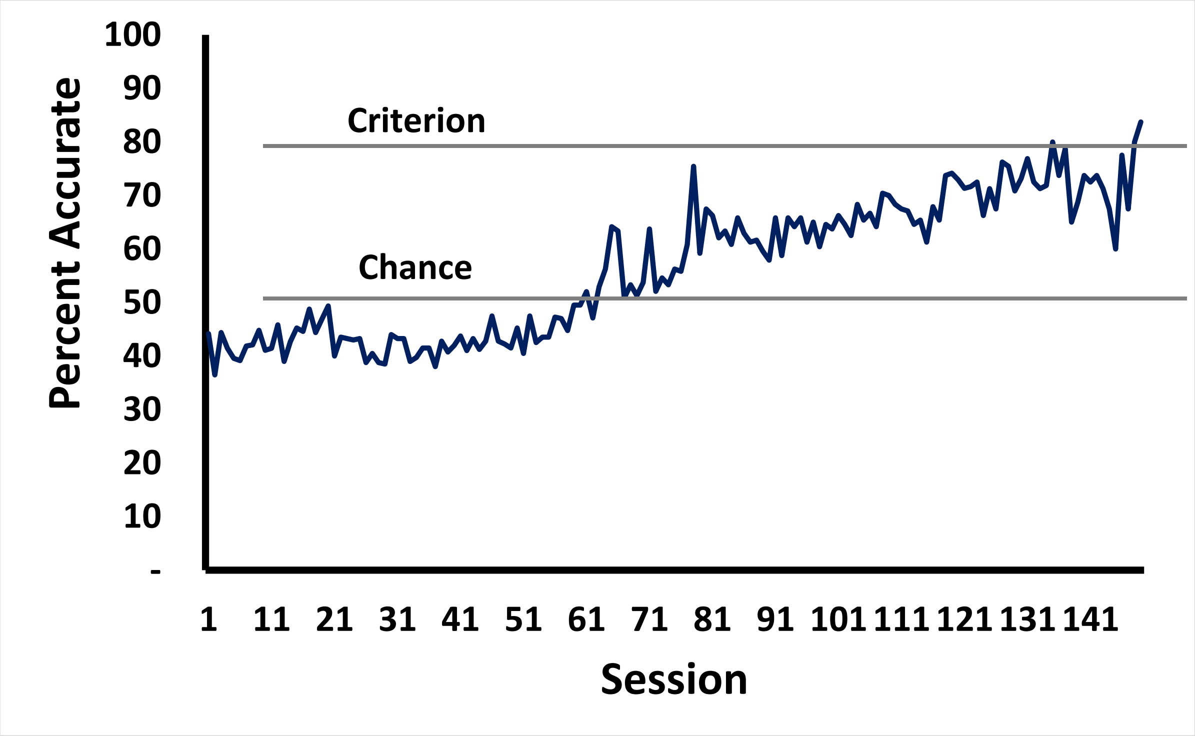

Figure 5: Average Learning Curve during Training

The percent accuracies for all subjects during training sessions. The training accuracies at criterion were significantly different from chance, indicating that the subjects learned the task.

Subjects	Right Short	Right Long	Left Short	Left Long	Overall
VO	86	86	67	96	84
TI	94	88	96	11	72
OS	95	95	96	57	86
DR	58	77	86	77	75
ME	68	44	87	86	71
Average	80	78	86	65	77

Table 2: Experiment 1 Accuracies

Percent correct during non-test trials for each subject in Experiment 1. Overall percent corrects were not significantly different from the criterion of 80%.

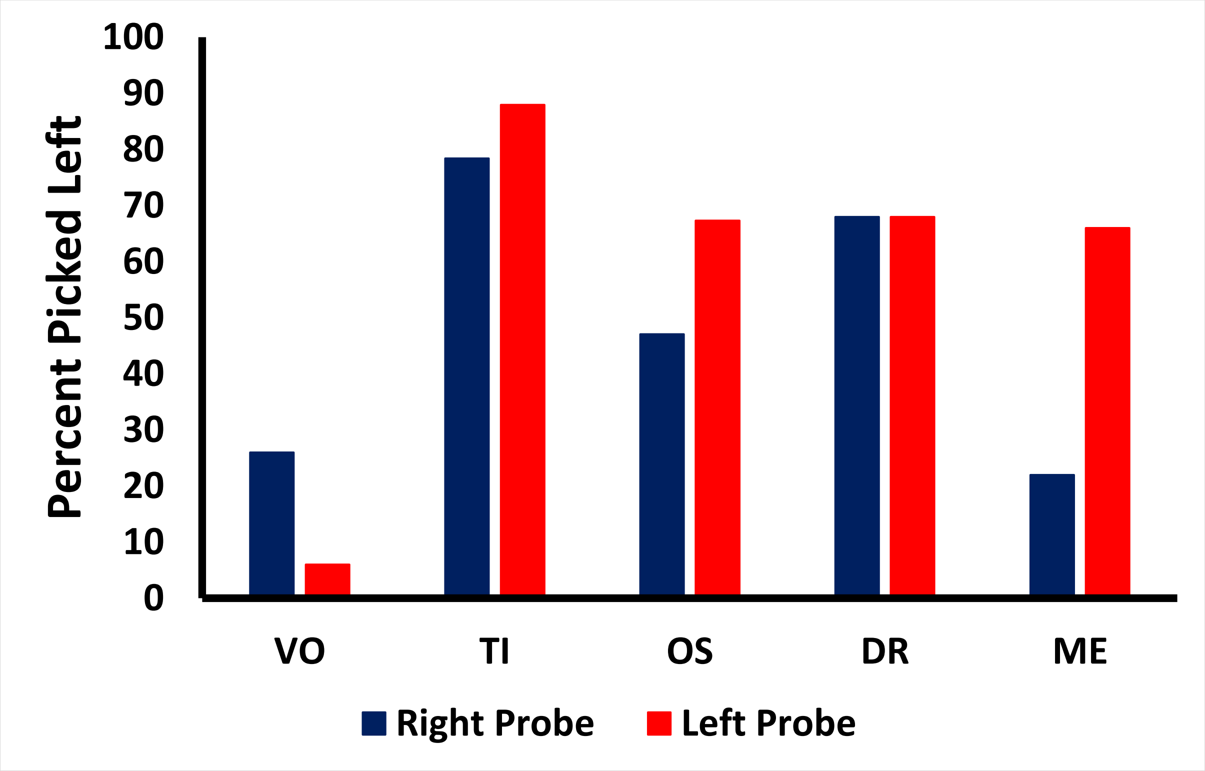

Figure 6: Experiment 1 Individual Percent Subjects Picked Left Purple Choice Boxes for Right and Left Probes

The percent each subject picked the left purple choice box across probe trial types. If the subjects displayed RM, then the percent picked left would be above 50% for Right Probes where the white square moved leftward and below 50% for Left Probes where the white square moved rightward. There was not a significant difference between picking left in Right Probes and picking left in Left Probes.

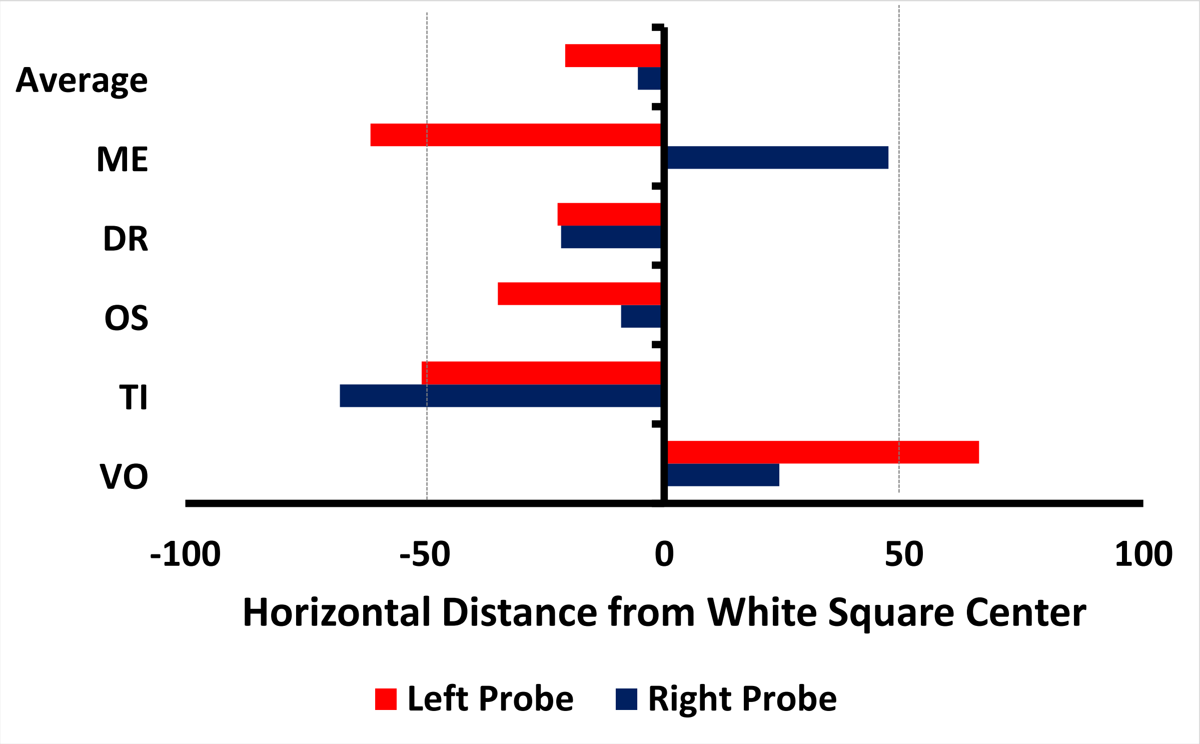

Figure 7: Experiment 1 Horizontal Displacements

The individual distances that each subject touched in pixels from the center of where the white square disappeared in Right and Left Probe trials. An absolute value over 50 indicates that subjects touched outside of the white square area. Negative values indicate touches left of the center and positive values indicate touches right of the center. The area within the dotted lines represents the area in which the subjects can touch to remain within the bounds of where the white square disappeared. There was no significant difference between the distances.

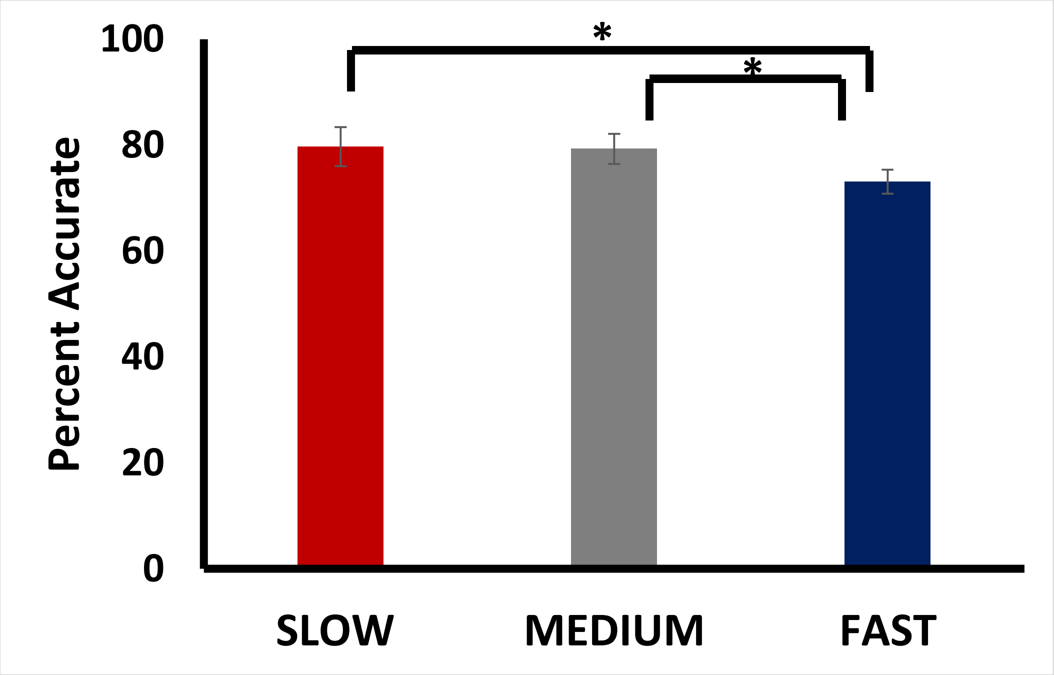

Figure 8: Experiment 2 Percent Accuracies across Session Speed

The overall percent accuracies averaged for all subjects across session speeds. The subjects were significantly less accurate during Fast sessions. Error bars are + – 1 SEM.

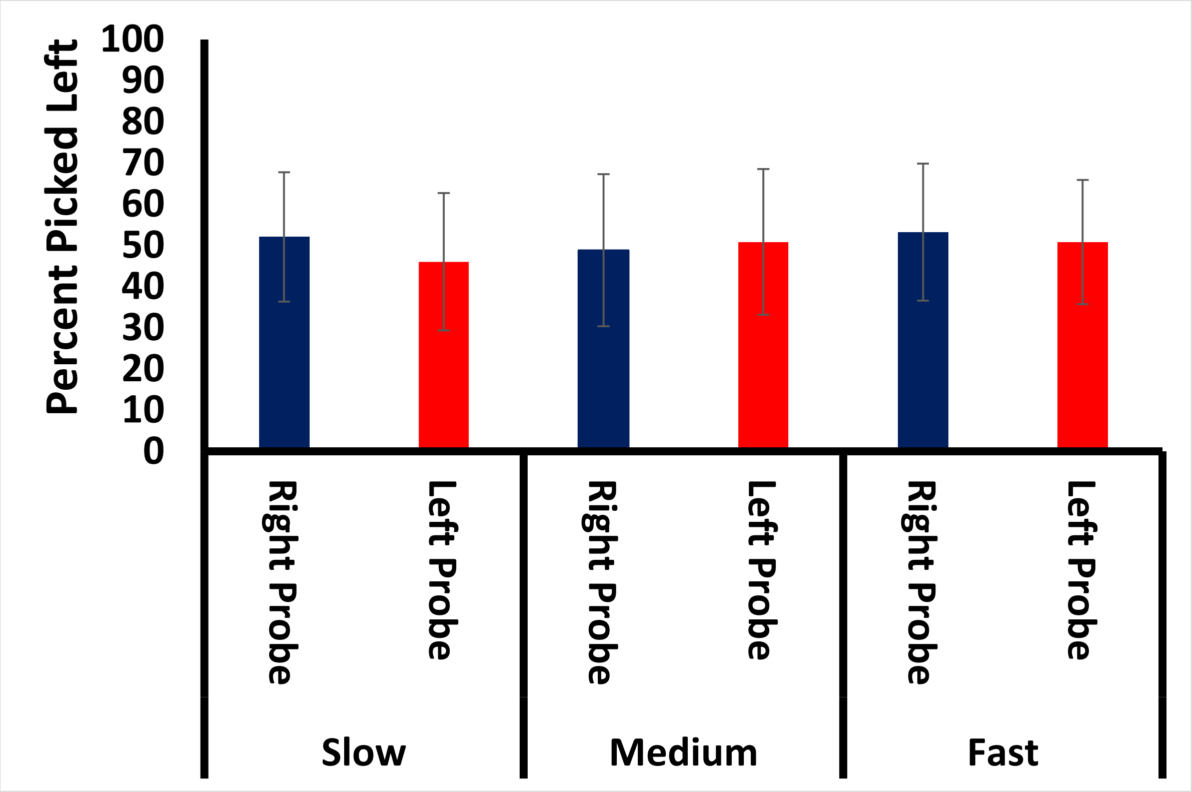

Figure 9: Experiment 2 Average Percent Subjects Picked Left Purple Choice Boxes for Left and Right Probes across All Speeds

The percent subjects picked left choice boxes across all speeds for Left and Right Probe trials. If the subjects displayed RM then they would have picked the left choice box >50% of the time during Right Probes and <50% of the time during Left Probes. There was no significant difference between picking left in Right Probes and picking left in Left Probes for any of the speed conditions. Error bars are + – 1 SEM.

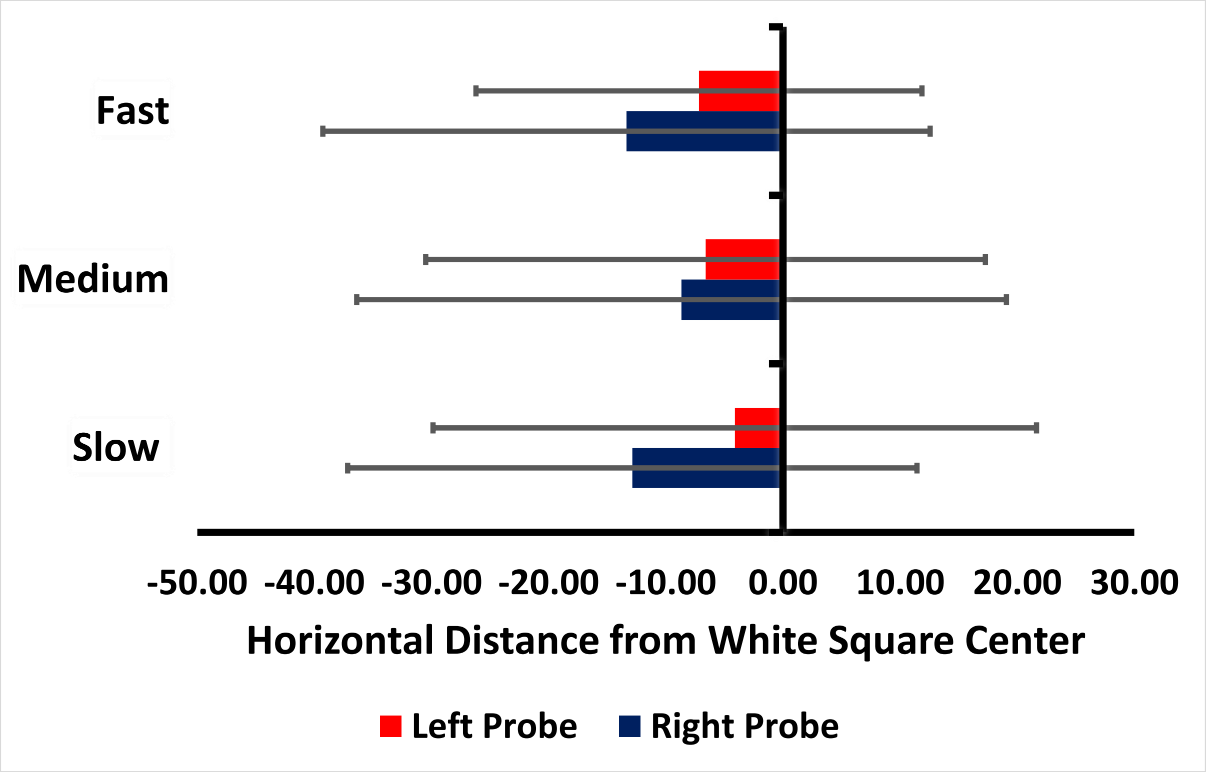

Figure 10: Experiment 2 Average Horizontal Displacements across Speeds

The average distance the subjects touched in pixels from the center of where the white square disappeared in Right and Left Probe trials. An absolute value of 50 indicates that subjects touched outside of the white square area. Negative values indicate touches left of the center and positive values indicate touches right of the center. Speed did not affect the horizontal distance between where the square disappeared and where subjects touched. Error bars are + – 1 SEM.