When going the right way is hard to do: Distinct phases of action compatibility in spatial knowledge development

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Abstract

The present study explores spatial knowledge development using online response measures available in mouse tracking. Online measures can reveal cognitive processing masked in post-processing measures. In the study, participants verified spatial descriptions by moving the mouse to a YES or NO button. Mouse tracking software (Freeman & Ambady, 2010) recorded mouse trajectories. Results demonstrated action-compatibility effects (ACE), differing as a function of spatial knowledge development. For well-developed spatial knowledge, the ACE reflected the physical spatial relationship (e.g. response button on right, but building to the left). In terms of temporal dynamics, this effect occurred later in the response. For less-developed knowledge, the spatial term drove the ACE (e.g., response button on right, but description used term left). In this case, the ACE was immediate and continuous. As would be consistent with learning, ACEs were observed more probably with proximal than distant locations. From these results, we infer that perceptuo-motor associations build with time and experience and can play an integral role in retrieval from well-developed spatial representations.

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1. Introduction

Recall your first few months in college. Early on you learned the locations of your dormitory and the dining hall. With time you became familiar with frequently visited buildings (the gym, the library, and your friends’ dorms) and your mental representation added more locations and connections between locations (Siegel & White, 1975). Learning the campus was grounded in your actions and perceptions; you made associations between the places you visited and the things you did and saw. How might these perceptions and actions shape spatial knowledge development? The extant literature on spatial knowledge development cannot answer this question, because it has largely measured spatial knowledge off-line rather than thinking about how space might entail situated simulation (Shelton & McNamara, 2004), or a mental re-experiencing of perceptual and motoric memories. To address this knowledge gap, we assessed whether online measures could reveal evidence of these simulations, and how the nature of these simulations may change as spatial knowledge develops.

1.1. Perceptuo-motor association in spatial representation

Single-cell recordings in animals suggest that spatial memory may incorporate perceptual and motoric traces of environmental experiences. Head-direction cells, observed in several mouse brain areas, fire when the animal's head faces a particular direction within a learned environment, regardless of the animal's body position (Taube, Muller, & Ranck, 1990). Associations between head-direction and landmarks build up during exploration and then guide navigation when re-entering the environment, even in the absence of visual landmark information (Taube, 2007; Zhang, 1996). When landmarks remain absent, head-direction cells build new associations, but also return quickly to original responses when a learned landmark reappears. The human equivalent of head-direction cell responses, which are in relation to vestibular and proprioceptive information, could be neural contributors to simulated spatial orientation (Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010).

Whereas studies have examined how navigators actively use perceptual and motoric information when learning environments (e.g., Brunyé & Taylor, 2008a; Mou, McNamara, Valiquette, & Rump, 2004; Wang & Spelke, 2002), few have explored how long-term spatial memories might incorporate perceptuo-motor information and how such information may guide spatial knowledge retrieval. In one study, Zetzsche, Wolter, Galbrath, and Schill (2009) had participants explore virtual environments that either complied with or violated...
Euclidean geometry (e.g., angles in a triangle summed to greater than 180°). Violations of Euclidean geometry should impede development of an abstracted, survey representation. Participants then had to find the shortest route from a new starting point in a test environment that also either complied with or violated Euclidean geometry. Results demonstrated that participants could successfully travel the shortest route without noticing Euclidean geometry violations. This suggests that navigation, instead of being based on abstracted, image-like representations, is primarily guided by representations that integrate sensorimotor information consistent with learning. In a study from our laboratory, Brunyé, Mahoney, and Taylor (2010) demonstrated that people use perceptuo-motor cues (footstep sounds) to shape spatial memories; when studying described routes, participants read faster and assumed they had walked farther when listening to fast relative to slow footstep sounds.

How might use of perceptuo-motor associations in memory change as spatial representations develop? Studies on spatial knowledge development to date cannot address this question as they have taken different approaches using different methodologies (Brunyé, Rapp, & Taylor, 2008; Brunyé & Taylor, 2008b; Evans, Marrero, & Butler, 1981; Foo, Duchon, Warren, & Tarr, 2007; Foo, Warren, Duchon, & Tarr, 2005; Hermer & Spelke, 1994, 1996; Montello, 1998; Pazzaglia & Taylor, 2007; Shelton & McNamara, 2004; Siegel & White, 1975; Taylor, Naylor, & Chechile, 1999; Thordyke & Hayes-Roth, 1982; Yeap & Jefferies, 2000; Zetzschke et al., 2009). Perhaps because the approaches differed, debates remain about how spatial knowledge progresses with time and experience (Evans et al., 1981; Hermer & Spelke, 1994, 1996; Montello, 1998; Siegel & White, 1975). One debated point revolves around the type of spatial information encoded as representations develop (e.g., Montello, 1998; Foo et al., 2005, 2007; Siegel & White, 1975). Does the represented information progress systematically from landmarks to routes to configurations (Siegel & White, 1975) or do these information types build into representations in parallel (Evans et al., 1981; Hermer & Spelke, 1994, 1996; Montello, 1998; Yeap & Jefferies, 2000)? Still another view suggests that spatial memories may not be simply isomorphic map-like mental structures, but rather preserve perceptuo-motor information about environmental experiences (Regier & Carlson, 2001; Taylor & Brunyé, in press; Tversky, 2005; Tversky & Hard, 2009). This latter notion contrasts with earlier theories positing that vast amodal connectionist networks code for spatial knowledge (Kuipers, 1978; McNamara, 1991; Stevens & Coupe, 1978).

If spatial representations incorporate perceptuo-motor associations, then the extent to which they do so should vary as a function of certain environment features. One of these features would be proximity between locations. People more likely interact perceptually and motorically with spatially proximal buildings than with distant ones. They see the relative location of two buildings with a slight turn of their head. People associate locations relative to coordinate axes of their body (Franklin & Tversky, 1990; Longo & Lourenço, 2007; Parsons, 1994; Tversky, 2005; Witt, Proffitt, & Epstein, 2004). For example, they process spatial relations in front of their body faster than those in back (Franklin & Tversky, 1990). For locations in close proximity, one can make these perceptuo-motor associations. Spatial language studies also suggest that during comprehension people integrate information about object proximity and object function (Carlson & Kenny, 2006; Logan & Sadler, 1996; Regier & Carlson, 2001). Actions related to specific objects appear to be represented and proximity between objects then facilitates responses to spatial utterances. In contrast, when landmarks are distant, people cannot make such associations and instead may draw on a more abstracted representation (Foo et al., 2005, 2007; Siegel & White, 1975). Travelers moving through an unfamiliar environment may orient on a distant landmark or use cardinal directions to guide navigation. Route planning studies also suggest that wayfinders rely on visual details to guide navigation within a proximal area, but on a coarse image-like representation for planning routes to distant spaces (Hölscher, Tenbrink, & Wiener, 2011; Wiener & Mallot, 2003). As distant landmarks are not readily associated to body motions, perceptuo-motor associations between distant locations may either not develop or may not have the same strength as those between proximal landmarks.

1.2. Online measures of embodied spatial cognition

Online measures of cognitive processing may provide insights into spatial knowledge development. Offline measures, such as map drawing, pointing, or spatial statement verification, reflect the end product of how people use their spatial representation. As such, they may reflect numerous cognitive operations, some strategic. In contrast, because online measures are closer in time to the cognitive process, they are less likely to reflect strategic processing. Online measures more likely reflect first-pass, immediate task analysis (e.g., Marslen-Wilson & Tyler, 1976). Comparisons of online and offline measures suggest that they tap different aspects of cognitive processing (e.g., Kempler, Almor, Tyler, Andersen, & MacDonald, 1998). To our knowledge, the present study is the first to use an online measure, mouse tracking, to explore spatial representations and their development. The program Mouse Tracker (Freeman & Ambady, 2010) records real time x-, y- coordinates of the computer mouse at an approximately 60–75 Hz sampling rate. Mouse trajectory data with this spatial and temporal fidelity should be sufficiently rich to discover perceptuo-motor traces involved in spatial memory retrieval.

Using mouse tracking to assess spatial representations draws on work taking an embodied approach (e.g., Glenberg & Kaschak, 2002; for reviews, see Barsalou, 2008; Fischer & Zwaan, 2008). Theories of embodied cognition suggest that knowledge representation captures the perceptions and actions associated with learning (e.g., Barsalou, 2008; Barsalou, Simmons, Barbey, & Wilson, 2003; Casteel, 2011; Fischer & Zwaan, 2008; Hommel, Müsseler, Aschersleben, & Prinz, 2001). Spatial knowledge can involve both perceptual (e.g., spatial position) and motor (e.g., orientating) information associated with learning. For example, when recalling the relative spatial relationship between locations, navigators might simulate orienting to one location and visualizing the other, similar to what they experienced when learning the environment. That is, when thinking about one location with respect to another, situated simulation would activate similar sensorimotor neural representations to those active when the environment was learned (Shelton & McNamara, 2004).

1.3. Action compatibility paradigm

Action compatibility paradigms may provide behavioral evidence of any tacit reactivation of perceptual and motor experiences during spatial memory retrieval. This reactivation has been referred to as motor resonance. Such paradigms have shown perceptuo-motor processing in language comprehension. For instance, in Zwaan and Taylor’s (2006) study, participants made sensibility judgments to sentences such as “Mark turned left at the intersection” more quickly when turning the response knob leftward compared to rightward. Such studies suggest that reading action words leads to mental simulation and motor resonance. If the motor resonance is compatible with concurrent motor processes, an “action-compatibility effect” (ACE) occurs (Glenberg & Kaschak, 2002), i.e. concurrent motor processes sharing directionality with the simulation can be facilitated and those incompatible with it can be impeded (Knoblich & Flach, 2001; Repp & Knoblich, 2004).

Studies on gestures in spatial cognition suggest a strong relation between spatial representations and hand movements (Alibali, 2005; Emmorey, Tversky, & Taylor, 2000; Hostetter & Alibali, 2008). Using spatial knowledge, particularly giving directions, frequently
involves hand movements. Although anecdotal, simply try describing a spatial layout while sitting on your hands. Many people in this situation have difficulty and some invoke head movements to compensate. In a more empirical approach, Emmorey et al. (2000) analyzed spontaneous gestures of individuals asked to describe a map they had just studied. Although this study's goal was to compare route versus survey description gestures, the important point for the current work is that all participants gestured. While the mapping between hand movements and spatial representations of buildings might not be as direct as with other actions and responses (e.g., giving or grasping objects), spontaneous gesture use with spatial descriptions, even to an imaginary conversational partner, strongly suggests a connection between hand movements and spatial representations.

Other research further strengthens this point. Other spatial description studies propose that gestures reflect spatial mental representations rather than the semantics of the spatial description (Goldin-Meadow & Beilock, 2010; Hostetter & Alibali, 2008; McNeil, 1992). When gestures are impeded, spatial descriptions become slower and less fluent. Further, people used different gestures when required to describe spatial information with different perspectives or diverse goals (Emmorey et al., 2000). Spatial problem solving, even without the goal to communicate to others, also elicits gestures (Kessell & Tversky, 2005).

Hints from the gesture literature suggest the connection between spatial knowledge retrieval and hand movements. As such, tracking mouse movements when verifying spatial relations might reflect how spatial knowledge integrates motor associations. Specifically, mouse tracking can be used to examine action compatibility, taking advantage of the fact that motor movements can reflect the qualitative nature of mental representations (Barsalou, 1999; Beilock & Holt, 2007; Fischer & Zwaan, 2008; Glenberg, 1997; Goldin-Meadow & Beilock, 2010). If spatial memory retrieval involves the reactivation of perceptuo-motor memory traces, then measuring mouse trajectories during spatial memory retrieval may show evidence of action compatibility. Further, mouse tracking can reveal the magnitude and time course of any compatibility effects (Freeman & Ambady, 2010; Richardson, Dale, & Spivey, 2007; Spivey, Richardson, & Dale, 2009).

One important issue should be noted. When presenting spatial information, situated simulations might not have a single basis. If motor resonance is activated by representations of spatial locations, the ACE would occur when the concurrent motion direction is congruent with the physical spatial relation. If the task is to verify a spatial relationship, however, to-be-related information needs to be conveyed so it can be verified. Processing even a simple directional term can activate the motor system (Hommel & Müsseler, 2006; Müsseler & Hommel, 1997a,b). Thus, when verifying a spatial description, motor resonance might also be activated by the semantic terms used. In this case, the ACE would occur when the direction of concurrent motion is congruent with the directional term. Thus, evidence of an ACE might have either a spatial and/or a semantic basis. Because adults would have extensive experience processing spatial terms, an ACE might have either a spatial and/or a semantic basis. Because adults would have extensive experience processing spatial terms, an ACE might have either a spatial and/or a semantic basis. Because adults would have extensive experience processing spatial terms, an ACE might have either a spatial and/or a semantic basis. Because adults would have extensive experience processing spatial terms, an ACE might have either a spatial and/or a semantic basis.

The present study used mouse tracking to explore two fundamental questions related to spatial representations and their development. These questions include: 1) do spatial representations show evidence of reactivation of perceptuo-motor memory traces developed during learning; 2) if so, does the nature of the perceptuo-motor trace change as the representation develops, i.e. with more time and experience. To examine motor resonance consistent with learning, participants verified relative spatial locations, both proximal and distant from one another, described through language. As detailed above, proximal locations should have more perceptual and motor associations. The study design also allows for the fact that spatial terms should elicit perceptual and motor associations (Glenberg & Kaschak, 2002) and that these can be disentangled from perceptual and motor associations elicited by spatial knowledge. To examine spatial representations at different development stages, we recruited undergraduates with varied campus experience, using experience level as a proxy for earlier and later stages of spatial knowledge development.

2. Method

2.1. Participants

Forty-nine Tufts undergraduates (23 males, 26 females) participated individually for monetary compensation. Participants included 22 first-years, 5 sophomores, 13 juniors and 9 seniors.

2.2. Stimuli and design

The stimuli consisted of names and pictures of fifty Tufts University buildings familiar to undergraduates. Building pictures, used to confirm front door locations, depicted the front-door side of the building, but avoided showing information about adjacent locations. Test trials used building names. On a given trial, participants saw two building names and a spatial term relating them (e.g., Dowling Hall, Eaton Hall, left). The experiment used a 2 (Familiarity: low, high) x 2 (Congruency: congruent, incongruent) x 2 (Proximity: proximal, distant) x 2 (Description Correctness: correct, incorrect) mixed-factor design. Description correctness, proximity, and congruency served as within-participant variables and familiarity served as a between-participant variable. Familiarity was operationalized by how long participants had been at Tufts. First-year and sophomore students comprised the low-familiarity group (27 participants); juniors and seniors made up the high-familiarity group (22 participants). Congruency, used to examine ACE, reflected the relation between the direction the mouse would be moved for an accurate response and the direction defined either by the spatial relationship between locations or the directional term. Response movement is spatially congruent if it is in the same direction as that defined by the spatial relationship between buildings. Semantic congruency compares mouse movement direction to the direction named by the spatial term (e.g., left). These different congruency definitions were separable for incorrect descriptions. For example, if the spatial description “Psychology building, Post office, right” is incorrect, the actual spatial relation between the buildings is to the left. A spatially-based ACE may attract mouse movement toward the left, the direction defining the spatial relationship. In contrast, a semantic-based ACE would attract mouse movement toward the right, in the direction the term describes. As fillers we included trials unrelated to leftward or rightward movement (“front” and “back”), but did not include these in any analyses. Proximity defined the physical proximity between buildings. Proximal trials described buildings physically adjacent to each other. Distant trials described buildings distant from and not within visible range of each other. Description Correctness reflected the described spatial relationship accuracy and was responded by either “Yes” (correct) or “No” (incorrect). Note that an incorrect description always described the spatial relationship as being opposite from the actual relationship, rather than in an orthogonal direction.
2.3. Procedure

Before beginning the formal experiment, participants viewed a list of Tufts buildings and verbally confirmed each building’s front door location. If they did not remember, the experimenter showed them the building picture depicting the front door. After confirming the front door for each building, participants began the spatial relationship trials, presented using MouseTracker 2.12 (http://mousetracker.jbfreeman.net/).

For each spatial relationship trial, a start button appeared, centered at the bottom of the 19-inch monitor. Participants clicked the start button and the reference building name appeared, centered on the screen for 1000 ms, followed below it by the target building name, for another 1000 ms, and finally below the target name a directional term (“left”, “right”, “forward” or “back”). Participants were to imagine facing the front door of the reference building and judge whether the directional term correctly described the relative location of the target building (e.g., Facing Dowling Hall, Eaton Hall is to your Left). 500 ms after the directional term appeared, the “YES”/“NO” response buttons appeared in the upper left and right corners and the mouse became active and visible. The building names, directional term, and response buttons remained visible until the participant responded. If participants responded accurately, the next trial started. For inaccurate responses, the program displayed an “X” for 1000 ms. When participants took longer than 5 s to respond, “time out” appeared. After each trial, the screen was blank for 500 ms before the next trial.

Participants completed 6 practice trials to familiarize themselves with the procedure. The experiment involved 100 trials, presented in random order, that included 10 trials each in the 8 conditions defined by the three within-participants variables (congruency, proximity and description correctness) plus 20 front/back filler trials. Half of participants had the “Yes” button at the upper right corner and the “No” button at the upper left corner, and half had the reverse placement. Both male and female participants completed the same procedure to examine gender effects.

2.4. Dependent variables and coding

Dependent variables included accuracy, response time (RT), and mouse trajectory data, all recorded by MouseTracker. Accuracy measured whether participants answered correctly. RT measured the time (ms) between participants clicking the start button and clicking the response button. We analyzed only RTs of correct responses. MouseTracker records the mouse’s raw position data (x–y coordinates) over time, allowing us to calculate three trajectory-related variables—initial time, area under the curve (AUC), and proportional Euclidean proximity (PEP). Initial time measured the time between when the mouse became active and the moment the participant first moved the mouse, potentially indicating participant confidence in their judgment. AUC is the area between the actual and an idealized trajectory, a straight line between the start and endpoint. Thus, positive AUC, with the mouse trajectory above the idealized trajectory, indicates mouse movement attracted toward the opposite response and negative AUC, with the mouse trajectory under the idealized one, indicates mouse movement attracted by the expected response. AUC directly demonstrates the extent to which mouse trajectories are attracted by the opposite response. PEP also measures the extent to which the mouse moved closer to the opposite response and is calculated as \((1 - \text{distance} / \text{max (distance)})\). “Distance” in the equation represents the Euclidean proximity between the mouse position at each time-step and the incorrect response button. More importantly, PEP allows an examination of the mouse movement’s temporal dynamics. To do so, we rescaled individual trial trajectories into a standard coordinate space and normalized them into 101 time-steps, using linear interpolation. We then combined the time-steps into five time bins (time-steps: 1–20, 21–40, 41–60, 61–80, 81–101) and averaged PEP for each time bin. Plots of trajectory data show the 101 time-steps. For ease in interpreting the graphs, the x-coordinates ranged from −1 to 1 and the y-coordinate ranged from 0 to 1.5 (with x- and y-axes intersecting at “−1, 0”).

3. Results

We eliminated six low-familiarity and two high-familiarity participants for low accuracy (less than .60). Preliminary analysis showed no effect of response button position or gender, so analyses collapsed across these variables. We analyzed correct and incorrect descriptions separately due to their interactions with the spatial and semantic definitions of congruency. Analyses of accurate responses, for both correct and incorrect descriptions, consisted of 2 (Familiarity: low, high) × 2 (Congruency: congruent, incongruent) × 2 (Proximity: proximal, distant) mixed model ANOVAs on accuracy, RT, initial times, and AUC data. The PEP analyses also included Time bin with 5 levels. Except for accuracy, only accurate responses were submitted into analyses. The mouse trajectory results, because they are central to the current study’s goals, were primarily analyzed and discussed. We only report significant effects here.

3.1. Correct descriptions

3.1.1. Mouse trajectory results

Mouse trajectory analyses showed an effect of congruency in AUC [F (1, 39) = 52.440, \(p < .001\), MSE = .194]. For correct descriptions, congruency reflects both spatially-based and semantically-based definitions. Consistent with the ACE, mouse movements were closer to the opposite response during incongruent [M = .561, SD = .697] than during congruent trials [M = .463, SD = .488] (see Fig. 1). In other words, when having to move the mouse in a direction opposite from the actual relative direction between landmarks or the direction described by spatial terms, mouse movement gravitated toward the spatially and semantically congruent response and away from the accurate response.

Examining the time-course of this response, the PEP data revealed an interaction between congruency and time bin [F (4, 156) = 5.148, \(p = .001\), MSE = .003]. Fig. 2 illustrates the degree to which the mouse traveled closer to the incorrect response over time. During incongruent trials, mouse trajectories showed more attraction to the opposite response, especially in the middle of the response (bin 3), compared to movement during congruent trials [F (1, 39) = 26.55, \(p = .001\)].

3.1.2. Accuracy and RT

For accuracy, responses to correct descriptions showed a marginal effect of proximity \([F (1, 39) = 3.176, p = .083, \text{MSE} = .016]\). Participants responded more accurately to proximal [M = .806, SD = .146] than to distant [M = .770, SD = .147] landmarks. Additionally, high-familiarity
Congruent participants [M = .828, SD = .137] responded more accurately than low-familiarity ones [M = .750, SD = .148, F (1, 39) = 8.423, p = .006, MSE = .029]. These main effects were qualified by an interaction between familiarity and proximity [F (1, 39) = 4.130, p = .049, MSE = .016]. Low-familiarity participants responded more accurately to proximal locations than distant ones [d = Mproximal − Mdistant = .076, F (1, 39) = 7.46, p = .009]; high-familiarity participants showed no proximity effect [d = Mproximal − Mdistant = -.005, F (1, 39) = .03, p = .862] (see Table 1 for means).

The accuracy results also showed an interesting, albeit marginal, three-way interaction between familiarity, proximity, and congruency [F (1, 39) = 3.478, p = .07, MSE = .014] (see Table 1 for means). As shown in Fig. 3, low-familiarity participants showed a marginal interaction between proximity and congruency [F (1, 39) = 2.84, p = .100, MSE = .04] such that the compatibility between the concurrent motion direction and spatial representation and/or directional term somewhat facilitated judgments of proximal locations [d = M incongruent − M congruent = −.072, F (1, 39) = 3.33, p = .067], but not distant locations [d = M incongruent − M congruent = .014, F (1, 39) = 25, p = .621]. No such interaction was evident with high-familiarity participants [F (1, 39) = .92, p = .343, MSE = .01].

The RT analysis also showed an effect of familiarity [F (1, 39) = 8.756, p = .005, MSE = 87452.455]. Consistent with the accuracy results, participants responded faster to proximal [M = 1739.639, SD = 494.554] than to distant landmarks [M = 1876.188, SD = .609.183].

3.2. Incorrect descriptions

3.2.1. Mouse trajectory results

Analysis of initial time showed an interaction between familiarity, spatial congruency, and time bin [F (1, 39) = 7.258, p = .010, MSE = 32236.602].

As Fig. 4 illustrates, low-familiarity participants took longer to start moving the mouse on semantically incongruent trials [d = M incongruent − M congruent = .80731, F (1, 39) = 4.25, p = .046] while high-familiarity participants took longer to start moving on spatially incongruent trials, although the difference was marginal [d = M incongruent − M congruent = 7.041, F (1, 39) = 3.07, p = .087] (see Table 2 for means). Keep in mind that for incorrect descriptions a spatially congruent trial is a semantically congruent trial.

The AUC results also showed an important three-way interaction between familiarity, proximity, and spatial congruency [F (1, 39) = 10.305, p = .003, MSE = .345] (see Table 2 for means). For proximal locations, high and low-familiarity groups showed opposite patterns with respect to spatial congruency, consistent with the initial time data [F (1, 39) = 13.915, p = .001, MSE = .410]. Specifically, high-familiarity participants showed a larger AUC [d = M incongruent − M congruent = .449, F (1, 39) = 4.92, p = .032] on spatially incongruent trials, while low-familiarity participants showed a larger AUC [d = M incongruent − M congruent = −.606, F (1, 39) = 9.41, p = .004] on semantically incongruent trials (see Fig. 5). Responses to distant locations showed no effects of familiarity or spatial congruency [F (1, 39) = .143, p = .708, MSE = .547].

The analysis of PEP revealed a four-way interaction between familiarity, proximity, spatial congruency, and time bin [F (4, 156) = 4.488, p = .002, MSE = .003]. Consistent with the AUC results, responses to proximal trials showed an interaction between familiarity, spatial congruency and time bin [F (4, 156) = 2.638, p = .036, MSE = .005]; no such interaction was found with distant locations [F (4, 156) = .084, p = .987, MSE = .004]. To further understand the 4-way interaction, we conducted a simple effects analysis examining proximal location data. The results of these analyses do not reach significance when accounting for multiple comparisons, but guide our interpretation of this complex and interesting interaction. The analysis suggests that low-familiarity participants had an interaction between spatial...
congruency and time bin \(F(4, 156) = 2.63, p = .037\), such that they moved closer to the opposite response on spatially congruent trials compared to spatially incongruent trials throughout time bins 2 \(F(1, 39) = 4.40, p = .042\), 3 \(F(1, 39) = 6.12, p = .018\), and 4 \(F(1, 39) = 5.22, p = .028\). Put another way, low-familiarity participants moved closer to the opposite response on semantically incongruent compared to semantically congruent trials. While this interaction did not reach significance for high familiarity participants \(F(4, 156) = 1.52, p = .198\), the response pattern suggests that high-familiarity participants moved closer to the opposite response on spatially incongruent trials only late in their response, in time bins 4 \(F(1, 39) = 3.08, p = .087\) and 5 \(F(1, 39) = 5.25, p = .027\), compared with mouse movement on spatially congruent trials. This interaction can best be seen in a graph of PEP difference scores (see Fig. 6), computed by subtracting the PEP of spatially congruent trials from that of spatially incongruent ones. In the graph, positive scores mean mouse movements on spatially incongruent trials were closer toward the opposite response more than those on spatially congruent trials; negative scores mean mouse movements on spatially congruent trials were closer to the opposite response than those on spatially incongruent trials. Thus, negative scores reflect an effect of semantic congruency.

### 3.2.2. Accuracy and RT

Accuracy analyses indicated that incorrect descriptions trials showed a proximity effect \(F(1, 39) = 7.863, p = .008, \text{MSE} = .020\). Opposite of the proximity effect with correct descriptions, participants made more errors with proximal \(M = .720, \text{SD} = .148\) than distant locations \(M = .782, \text{SD} = .145\). In addition, high-familiarity participants \(M = .788, \text{SD} = .131\) responded more accurately (although not more quickly) than low-familiarity participants \(M = .715, \text{SD} = .158, F(1, 37) = 5.922, p = .020, \text{MSE} = .036\). No other effects were found on RT or accuracy.

### 4. Discussion

The present study used a novel online processing measure, mouse tracking, to explore fundamental questions about spatial representations and their development. Participants with either extensive or more limited environment experience verified relative spatial locations using a computer mouse, and we tracked their movement trajectories towards a response. Results strongly suggest action-based compatibility effects (ACEs) when retrieving spatial information to verify spatial relations. These action-based influences appear to have distinct sources as a function of spatial representation development, being spatially driven with high-familiarity and semantically driven with low-familiarity. Additionally, spatial proximity, because of its implications for perceptual and motor interactions, also affected evidence of perceptuo-motor information retrieval.

#### 4.1. Online spatial knowledge processing

The present results suggest that spatial knowledge retrieval reacts to perceptual and motor experiences consistent with learning. As shown in Fig. 5, when correctly rejecting incorrect spatial descriptions of well-learned environments, participants with the NO button in the same direction as the relative spatial location (spatial congruent condition), mouse movements converged on this correct response, with little deviation in the opposite direction. For participants with the NO button in the opposite direction (spatially incongruent condition), mouse trajectories tended toward the opposite response. The initial time measure, while marginally significant, further suggested that high-familiarity participants might be more confident about their response on spatially congruent trials compared to the spatially incongruent ones (see Fig. 4). This finding is consistent with findings suggesting embodiment in language processing (Glenberg & Kaschak, 2002; Tucker & Ellis, 2004; Zwaan & Taylor, 2006) and extends to spatial knowledge retrieval.

Many studies showing ACEs have explored language processing. From this work, Glenberg and Kaschak (2002) proposed a connection between language comprehension and motor processes. Other work has applied the ACE to visual processes, showing an interaction between current motor responses and visual stimulus position, named the spatial Stroop effect (Lu & Proctor, 1995; Simon, 1990; Zhao, Chen, & West, 2010; Zwaan & Taylor, 2006; Zwaan & Yaxley, 2003). For example, people respond more slowly when the visual target and response key are in opposite directions, even when target position is irrelevant to the required response. The present study extends the connection between cognitive and motor processing to spatial representations of environments. While response button positions in the present study did not directly relate to the spatial relationship judgments,

#### Table 2

<table>
<thead>
<tr>
<th>Incorrect description</th>
<th>Low-familiarity group</th>
<th>High-familiarity group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Proximal</td>
<td>Distant</td>
</tr>
<tr>
<td></td>
<td>Congruent</td>
<td>Incongruent</td>
</tr>
<tr>
<td>RT (SD)</td>
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<td>Accuracy (SD)</td>
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<td>Initial time (SD)</td>
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<td>AUC (SD)</td>
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</table>

Fig. 4. Interaction between familiarity and congruency in initial time of rejecting incorrect descriptions.
Curvature Area of development (see Figs. 4 suggesting that the ACE has distinct sources at early and later stages of development.

Interestingly, the mouse trajectory measure converged, strongly supporting the compatibility between the motor response and mental representation. Movements tended in a direction consistent with the relative spatial location, at least when rejecting incorrect spatial descriptions with well-developed spatial knowledge.

4.2. Embodied processing of spatial knowledge development

The present study also explored how reactivation of perceptual and motor experiences may change as spatial representations develop. Interestingly, the mouse trajectory measure converged, strongly suggesting that the ACE has distinct sources at early and later stages of development (see Figs. 4–6). Incorrect spatial descriptions allowed us to disentangle spatial and semantic sources of motor resonance. Results showed that high-familiarity participants based judgments on stable spatial representations that associated landmarks to their own imagined location. In this case, mouse trajectories in spatially compatible trials moved more directly to the correct response, compared with those attracted by the incorrect response in spatial incompatible trials. In contrast, motor resonance for low-familiarity participants appeared to arise from associations to the spatial term (e.g., moving more left to the term left). Other studies have similarly shown that reading directional words activates corresponding perceptual or motor representations (Zwaan & Yaxley, 2003; Hommel & Müßeler, 2006; Müßeler & Hommel, 1997a,b; Chao & Martin, 2000; Pulvermüller, 1999). In summary, retrieving information from well-learned environments leads to spatially-defined motor resonance while retrieving information from less-well-learned environments shows semantically-defined motor resonance.

What stands out in our findings is that spatially-based motor resonance appears to eclipse its semantic-based counterpart for well-learned environments. With increasing environment experience, associations between spatial locations and navigators’ sensorimotor processes become solidified and recalling relative spatial information then invokes motor resonance. Motor simulations based on well-developed spatial associations appear to “outweigh” associations to spatial terminology. In contrast, less-developed spatial representations have not built solid spatial associations, so motor resonance for these navigators is linked to the well-learned spatial terms (“left” or “right”). In summary, the present study indicates that with increasing familiarity:

- High-familiarity participants based judgments on stable spatial representations that associated landmarks to their own imagined location.
- Low-familiarity participants appeared to arise from associations to the spatial term (e.g., moving more left to the term left).

The compatibility between the motor response and mental representation affects responses. Movements tended in a direction consistent with the relative spatial location, at least when rejecting incorrect spatial descriptions with well-developed spatial knowledge.

Fig. 5. Three-way interaction between familiarity, proximity and congruency in AUC (a) of rejecting incorrect descriptions. Mouse trajectories for proximal trials help explain this interaction and are thus plotted as real-time figures: b) for high-familiarity group, mouse trajectories for incongruent trials show a continuous attraction to “yes” response; b) for low-familiarity group, mouse trajectories for congruent trials show a continuous attraction to “yes” response. Note that mouse trajectories for participants with “YES” and “NO” buttons in opposite positions have been collapsed to the present position for ease of illustration.

Fig. 6. Difference scores between incongruent and congruent conditions (incongruent–congruent) in PEP for rejecting incorrect descriptions are plotted as a function of normalized time, separately for proximal (a) and distant (b) location pairs. For proximal trials (a), mouse trajectories of low-familiarity participants were closer to incorrect response in congruent condition throughout time-course (negative value), while those of high-familiarity participants were closer to incorrect response in congruent condition at late stage of mouse movement (positive value).
experience human spatial knowledge builds associations between spatial locations that include perceptual and motor associations.

4.3. Temporal dynamics of perceptuo-motor simulations

By using online measures, the present study revealed the temporal dynamics of perceptuo-motor associations when processing spatial knowledge. Our PEP measure to incorrect spatial descriptions suggested different temporal dynamics as a function of spatial knowledge development (see Fig. 6). For low-familiarity participants, whose ACE appears semantically based, the ACE started early and extended throughout the response period. This suggests immediate and lasting motor resonance to spatial language. For high-familiarity participants, who showed spatially-based ACEs, effects of motor resonance appeared later. This later effect suggests that accessing spatial relation information takes longer than accessing a spatial term’s semantic meaning. People would have had a lifetime of experience with the spatial terms and less so with the Tufts campus. In addition, Fig. 6(a) shows that mouse trajectories of high-familiarity participants gravitated toward the semantically congruent response at time bin 2, although the effect was not statistically significant. This weak effect may also support earlier semantic processing, even when retrieving well-developed spatial knowledge. But with well-learned environments, motor resonance based on semantic processing appears to be inhibited or attenuated.

Previous studies showing ACEs in language comprehension primarily relied on post-processing response time measures (Glenberg & Kaschak, 2002; Zwaan & Taylor, 2006). However, the present study’s comparable measure did not show a congruency effect. Instead evidence of ACEs with spatial knowledge appeared in mouse trajectories. This post-processing/on-line processing difference has several possible explanations. One explanation involves strength of associations. Language processing, with all the experience participants have using language, may result in stronger and more lasting motor resonance that can be easily detected by post-processing measures. Compared to processing spatial terms, perceptuo-motor simulation activated when retrieving spatial knowledge may not have the same strength of association and may only be evident in online measures. Second, the different sources of perceptuo-motor associations, spatial and semantic, resulted in ACEs in opposite directions for incorrect spatial descriptions, thereby potentially washing out response time effects. Thus, mouse tracking may provide means for examining mechanisms of embodied processing masked by offline measures.

4.4. Spatial proximity and ACE

As predicted perceptuo-motor associations varied as a function of spatial proximity: participants verified both proximal and distant locations. People would have more perceptual (see buildings together) and motor (point to one building from the other or turn the body to face the building) experiences with proximal, compared to distant, locations. Thus, they are more likely to associate proximal locations using their body’s coordinate axes (Franklin & Tversky, 1990; Longo & Lourenco, 2007; Parsons, 1994; Witt et al., 2004). As Fig. 3 illustrates, accuracy when processing correct spatial descriptions benefited from spatial and semantic congruency for low-familiarity participants. With proximal locations, they had a higher accuracy in congruent condition, compared to incongruent condition, while no such facilitation of compatibility was found with distant locations. Further, the interaction between proximity, congruency, and familiarity when rejecting incorrect spatial descriptions suggested action compatibility primarily when processing proximal locations. No ACE was observed with distant locations, regardless of environmental experience. This result seems to contradict the semantic-based ACE for the low-familiarity group. If the ACE for low-familiarity participants arises from spatial term comprehension, then they should also demonstrate an ACE with distant locations. However, the lack or an ACE with distant locations may imply differential cognitive processing for proximal and distant spatial information. We did not observe an ACE for either high- or low-familiarity participants with distant locations when rejecting spatial relations. People may relate distant locations spatially, even during initial environment learning (Holscher et al., 2011; Wiener & Mallot, 2003). Alternatively, people may create mental snapshots (Shelton & McNamara, 2001) that include proximal locations in a single mental image that maintains the relative locations, as well as perceptual and motor associations. Distant locations would be difficult to represent this way. In this case, ACE differences between proximal and distant locations would reflect differences in how they are represented, rather than effects of the learning experience. Previous findings from our lab suggest that a required retrieval perspective affects information retrieved from the spatial representation in a perspective-consistent manner (Brunyé, Mahoney, Gardony, & Taylor, 2010; Taylor et al., 1999). This interpretation would be akin to the SNARC effect (Dehaene, Bossini, & Giraux, 1993) wherein people represent Arabic numbers as if on a mental image of a number line. The consequence of this representation is that people respond faster to relatively larger numbers with the right hand, and faster to smaller numbers with the left hand, even when number magnitude is task-irrelevant. However, these interpretations are speculative and will be explored further in later studies.

It should be noted that we did not observe the interaction between congruency and proximity when participants confirmed spatial relations. Instead, with correct spatial descriptions, participants’ mouse trajectories showed a congruency effect, suggestive of embodiment, across proximal and distant locations (see Figs. 1 & 2). Thus, representations of distant locations may still involve some perceptuo-motor simulation. However, the source of this embodiment, whether spatial or semantic, cannot be disentangled and the ACE may reflect one or both of these sources.

4.5. Conclusion

To summarize, retrieving spatial knowledge of a well-learned environment appears to activate perceptual and motor simulations reflecting sensorimotor experiences when learning the environment. These simulations are built on dynamic association between navigator and landmarks formed during learning and increasing with environmental experience. With less experience, motor simulations draw on other, well-learned associations, in this case perceptuo-motor associations to spatial terms, such as left. By adopting on-line processing measures, findings from this study provide unique evidence of different sources for perceptuo-motor simulation in spatial memory, the effects of which unfold differently over time.

References
