

## RESEARCH ARTICLE

# More than a feeling: incidental learning of array geometry by blindfolded adult humans revealed through touch

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### SUMMARY

**View-based matching theories of orientation suggest that mobile organisms encode a visual memory consisting of a visual panorama from a target location and maneuver to reduce discrepancy between current visual perception and this stored visual memory to return to a location. Recent success of such theories to explain the orientation behavior of insects and birds raises questions regarding the extent to which such an explanation generalizes to other species. In the present study, we attempted to determine the extent to which such view-based matching theories may explain the orientation behavior of a mammalian species (in this case adult humans). We modified a traditional enclosure orientation task so that it involved only the use of the haptic sense. The use of a haptic orientation task to investigate the extent to which view-based matching theories may explain the orientation behavior of adult humans appeared ideal because it provided an opportunity for us to explicitly prohibit the use of vision. Specifically, we trained disoriented and blindfolded human participants to search by touch for a target object hidden in one of four locations marked by distinctive textural cues located on top of four discrete landmarks arranged in a rectangular array. Following training, we removed the distinctive textural cues and probed the extent to which participants learned the geometry of the landmark array. In the absence of vision and the trained textural cues, participants showed evidence that they learned the geometry of the landmark array. Such evidence cannot be explained by an appeal to view-based matching strategies and is consistent with explanations of spatial orientation related to the incidental learning of environmental geometry.**

Key words: learning, orientation, geometry, view-based matching, haptic.

Received 9 August 2012; Accepted 8 October 2012

### INTRODUCTION

Orientation and navigation are daunting tasks that are critical for survival and reproduction, and fundamental to these processes is an estimation of current position (Gallistel, 1990). Spatial coding of position is defined with respect to how spatial locations are referenced – either with respect to the self (i.e. egocentric) or with respect to each other (i.e. allocentric) (for reviews, see O’Keefe and Nadel, 1978; Burgess, 2006). Within the last 30 years, a substantial amount of literature on the ability of mobile organisms to orient in enclosed spaces has been interpreted as evidence for allocentric coding (for reviews, see Cheng and Newcombe, 2005; Vallortigara, 2009; Tommasi et al., 2012). Specifically, almost every organism at almost any stage of development that has ever been trained to approach a distinctive visual cue that marks the location of a hidden target object (such as food) in a corner of a rectangular enclosure has been equally likely to approach the trained corner and its 180 deg rotational equivalent when the distinctive visual cue was removed during testing (for reviews, see Cheng and Newcombe, 2005; Vallortigara, 2009; Tommasi et al., 2012). This finding is often referred to as the ‘rotational error’ phenomenon (Cheng, 1986; Gallistel, 1990).

Such equivalent responding to the trained and rotational equivalent locations has been taken as evidence that mobile organisms learn about the geometric shape of the environment (i.e. learned about the unique metric relations such as the distances

between surfaces and angles formed by surfaces of the enclosure) (for a review, see Gallistel, 1990). The logic is that in the absence of the visual cue coupled with an absence of learning about environmental geometry, responding should be allocated equally to all four corners of the enclosure. However, the rotational error phenomenon is pervasive across both phylogeny and ontogeny, and suggests that learning of environmental geometry is a fundamental and ubiquitous component of orientation (for reviews, see Cheng, 2005; Cheng and Newcombe, 2005; Vallortigara, 2009; Tommasi et al., 2012).

Learning of the geometric shape of the environment (evidenced by above-chance responding to the trained and rotational equivalent locations) occurs incidentally – that is, it occurs despite being neither necessary nor sufficient for successful determination of the target object during training (Eysenck, 1974; Doeller and Burgess, 2008). Specifically, a process of beaconing (i.e. movement towards a landmark) to the visual cue is both necessary and sufficient for determination of the target object, and beaconing need not involve learning of geometric relations (Cheng, 2012). Furthermore, this learning about environmental geometry is not susceptible to associative cue competition (i.e. blocking or overshadowing) and has been shown to involve distinct brain regions (Cheng, 1986; Cheng, 2005; Doeller and Burgess, 2008; Doeller et al., 2008).

Interestingly, incidental learning of environmental geometry does not appear to be constrained to environments with extended

surfaces (i.e. enclosures). Various animals have been shown to extract geometric properties from an array of discrete landmarks. Specifically, rats (Gibson et al., 2007), domestic chicks (Pecchia and Vallortigara, 2010a; Pecchia and Vallortigara, 2012), pigeons (Sturz and Katz, 2009), nutcrackers (Kamil and Jones, 1997; Kamil and Jones, 2000), and adult humans (Sutton et al., 2012) appear to be able to orient with respect to the geometric configuration of a visual landmark array. An ability to orient with respect to the geometric properties of a landmark array has been taken as evidence for the involvement of the same mechanism as in learning enclosure geometry while providing converging evidence for the fundamental nature of geometric information in spatial learning (e.g. Gibson et al., 2007; see also Doeller and Burgess, 2008).

More recently, some research has challenged the notion of the allocentric and incidental learning of the geometric properties of the environment (for a review, see Cheng, 2008). Derived from an expansive literature on insect navigation (Collett and Zeil, 1998; Cheng, 2012), various iterations of a view-based matching theory have emerged to explain the rotational error phenomenon without need to posit allocentric coding or incidental learning of geometric shape (Cheng, 2008). Egocentric in nature, these view-based matching theories propose that mobile organisms store a visual memory consisting of a visual panorama from the target location. To return to that location, one compares current visual perception with this stored visual memory and maneuvers to reduce the discrepancy. Mounting evidence suggests that insects and birds may accomplish successful orientation with respect to enclosures and landmark arrays in such an egocentric fashion (Stürzl et al., 2008; Wystrach and Beugnon, 2009; Pecchia and Vallortigara, 2010b; Pecchia et al., 2011; Pecchia and Vallortigara, 2012; cf. Lee et al., 2012).

The success of these view-based matching theories to explain the rotational error of insects and birds raises questions regarding the extent to which such an explanation generalizes to other species. For example, it remains possible that the rotational error phenomenon obtained with other mobile organisms can also be explained by an egocentric strategy of view-based matching. In the present study, we attempted to determine the extent to which such view-based matching theories may explain the orientation behavior of a mammalian species (in this case adult humans); however, we modified the traditional enclosure orientation task so that it involved only the use of the haptic sense. The use of a haptic orientation task to investigate the rotational error phenomenon (and by extension the extent to which view-based matching theories may explain the orientation behavior of adult humans) appeared ideal because it provided an opportunity for us to explicitly prohibit the use of vision.

Given that various animals appear capable of successful orientation and navigation in the absence of vision (for reviews, see Etienne et al., 1996; Healy, 1998; Avni et al., 2008), an investigation of orientation in the absence of vision also appeared critical in determining the generality of learning mechanisms across species and illuminating the extent to which an effect in one sensory modality is obtained in another sensory modality. Specifically, comparative researchers have long been interested in determining the generality of learning mechanisms across species (Bitterman, 1960; Bitterman, 1975). Moreover, the extent to which an effect in one sensory modality is obtained in another sensory modality has a rich history of illuminating potential similarities or differences in the underlying learning mechanisms (for reviews, see Ettliger and Wilson, 1990; Neath and Surprenant, 2005). Within these contexts, recent empirical efforts have focused on haptic spatial learning (for a review, see Lederman and Klatzky, 2009); yet, to date, evidence

for the rotational error phenomenon has been constrained to visual orientation tasks (Cheng, 2005; Cheng and Newcombe, 2005; Vallortigara, 2009; Tommasi et al., 2012).

Much of the research regarding haptic spatial learning has focused on peripersonal space (i.e. space immediately surrounding the body) and revealed that participants are able to learn geometric properties (such as distance, size and curvature) of objects (Henriques and Soechting, 2003; Lederman and Klatzky, 2009). Only relatively recently has research focused on learning of object layouts in larger space; for example, place learning (i.e. the ability to return to a location) using landmarks has been shown to occur by mechanical contact alone (Harrison and Turvey, 2010). Such a result provides evidence that spatial models developed to account for visual spatial learning (for reviews, see Cheng and Spetch, 1998; Healy, 1998; see also Sturz et al., 2011a) may also apply to haptic spatial learning.

In the current experiment, we trained disoriented and blindfolded adult human participants to search by touch for a target object hidden on top of one of four discrete landmarks each marked with a distinctive textural cue arranged in a rectangular array (see Fig. 1). Given the repeatedly demonstrated ability of human participants to identify objects *via* touch (Lederman and Klatzky, 2009), participants should be capable of associating a unique texture with the target object relatively rapidly. The central question was whether participants also learned about the geometry of the landmark array despite being neither necessary nor sufficient for successful determination of the target object. To that end, after reaching a specified training criterion, we removed the distinctive textural cues and probed the extent to which they learned the geometry of the landmark array. Should participants respond to the correct and rotationally equivalent locations at above-chance levels in the absence of distinct textural cues (i.e. demonstrate the rotational error phenomenon *via* touch), it would provide evidence that participants learned the geometric properties of the landmark array. Specifically, it would provide evidence that they learned about the geometric configuration of the landmarks during training despite being neither necessary nor sufficient for the determination of the target object. Importantly, evidence for this learning about the geometric configuration in the absence of vision could not be undermined by appealing to strict view-based matching because view-based matching (by definition) would require visual input in order to encode a visual memory, to have access to current visual perception, and to reduce any discrepancy between current visual perception and any stored visual memory. By explicitly prohibiting the use of vision during the orientation task, we have eliminated the possibility to encode a visual memory, to have access to current visual perception, and/or to reduce the discrepancy between current visual perception and a stored visual memory. As a result, the use of a strict egocentric view-based matching strategy would predict equivalent searching at all four locations in the absence of the trained textural cue (i.e. no evidence for the rotational error phenomenon).

## MATERIALS AND METHODS

### Participants

Twenty-five undergraduate students served as participants (12 males and 13 females). Of participants that provided dominant hand information ( $N=21$ ), 90% reported being right-handed and the remaining 10% reported being left-handed. Participants had normal sensorimotor abilities. Participants received extra credit or participated as part of a course requirement. One female participant did not meet training criteria (see below) and was excluded from

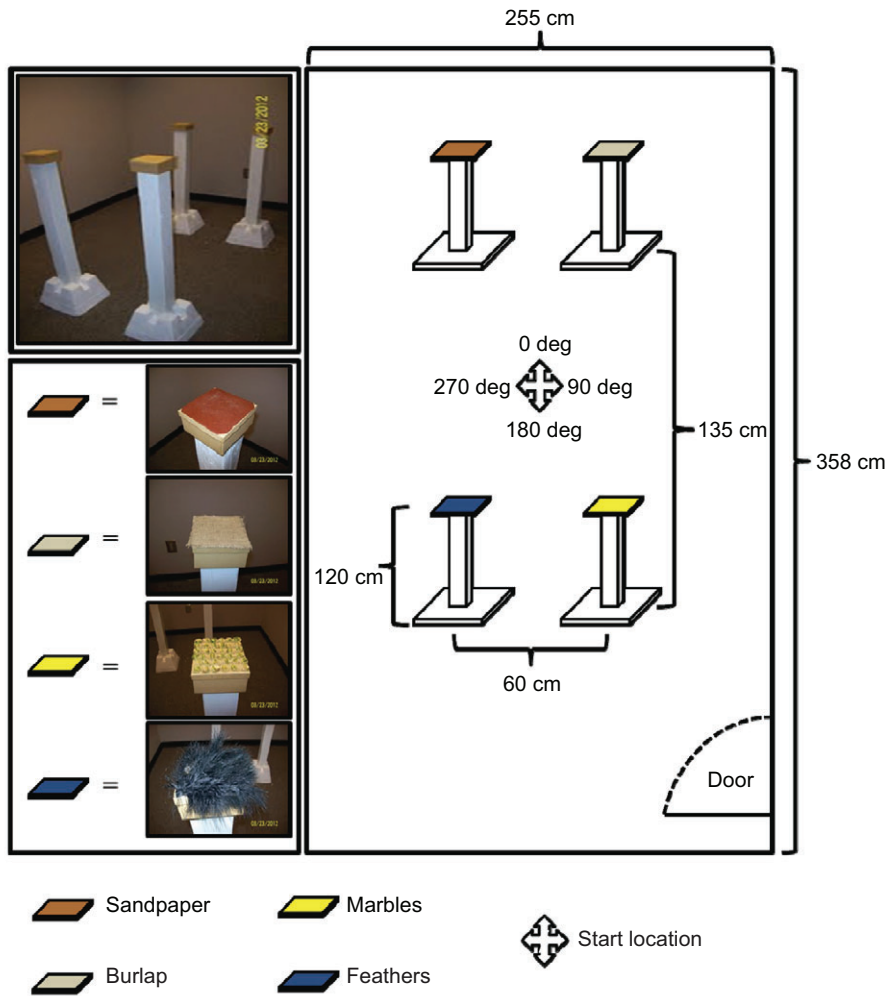


Fig. 1. Images (left-hand panels) and schematics (right-hand panel) of the landmark array, textures and experimental room. For illustrative purposes, textures are colored and start position is marked. Please note that schematics are not to scale. Please also note that textures were present during all training trials but absent during the testing trial (see text for details).

all analyses. The remaining 24 participants (12 males and 12 females) were included in all analyses.

This research was conducted following the relevant ethical guidelines for human research.

#### Apparatus and stimuli

All experimental events occurred in a room that measured 358×255 cm (Fig. 1). Four identical wooden posts served as landmarks. Each post measured (9.00×9.00×92.00 cm, length × width × height) and was affixed to a concrete Dek-Block that measured 27.80×27.80 cm at the base and 20.10×20.10 cm at the top (with a height of 20.20 cm). The total height of each landmark was 112 cm. Each post was sanded and painted white to eliminate the chance of injury. A small cardboard box (12.00×12.00×4.00 cm, length × width × height) was affixed to the top of each post. The lid of each cardboard box was removable. During ‘training’ (see below), the tops were covered with four distinct textures (clockwise from top left to bottom left in Fig. 1: sandpaper, burlap, marbles, feathers). The textures remained in these locations with respect to the landmark array for the duration of training (see below). During ‘testing’ (see below), the textured cardboard tops were replaced with four identical blank (i.e. cardboard only) tops. A wooden block (5.08×2.22×2.54 cm, length × width × height) served as the target object. The four wooden posts were arranged in a rectangular array that measured 60×135 cm (see Fig. 1).

#### Procedure

In a briefing room, participants were provided with task instructions. Participants were informed that their task would be to first touch four textures located on top of wooden posts. After touching the textures, they would search for a small wooden block that was hidden in a small box below each texture. Participants were informed that they would select a container by removing the lid of the box and inserting their hand into the box. Participants were also informed that all of this would occur while blindfolded. Finally, participants were informed that they would continue the experiment until they located the wooden block six times in a row on their first choice (i.e. six consecutive correct first choices) or until 50 min had elapsed. Participants were then blindfolded and led into the experimental room containing the landmark array.

#### Training

Before the experiment, a randomly selected landmark (including its textured top) was designated as the rewarded landmark (i.e. contained the target object) for that particular participant for the duration of training. The wooden block was then placed in the cardboard box of the designated trained landmark. An equal number of males and females were trained at each landmark (including its textured top). As a result, each of the four textural cues served as the rewarded landmark for three males and three females.

Prior to the start of each trial, we attempted to disorient the blindfolded participants by leading them around the experimental room (outside of the landmark array) in a circuitous route. The circuitous route terminated in the center of the landmark array (i.e. start position) facing a random direction from 0 to 270 deg in increments of 90 deg for each trial (see Fig. 1). Participants then touched all textures and began their search for the target object. Participants searched until they located the target object.

After participants located the target object, the experimenter retrieved the target object and led the participant outside of the landmark array. The experimenter then returned the textured tops to their original position and inserted the wooden block back into the rewarded location (being sure to replace the tops to their original position in a random order from trial to trial, to prevent learning location based upon sound). Participants were then led on the circuitous route that terminated at the start position facing a random direction. This process was repeated for each trial. Each time a participant located the target object on his or her first choice, the experimenter informed the participant of his or her current consecutive correct first choices. Once participants located the wooden block five consecutive times on their first choice, testing began. Note that participants believed they were required to find the target object once more on their first choice when testing began.

#### Testing

Testing consisted of one trial. Testing was conducted in a manner identical to training with the exception that the textured tops were replaced with blank tops (i.e. cardboard only) when placed back in position on top of the boxes affixed to the landmarks. As a result, landmarks were devoid of all textural cues present during training. Moreover, the target object was absent. After being led on the circuitous route that terminated at the start location facing a random direction (as in training), participants began their search (as in training). Because the target object was absent, we terminated the search process after each participant's fifth search.

#### Attempt to confirm disorientation

We attempted to confirm that participants were disoriented (or at least not oriented with respect to the only conspicuous feature of the experimental room – the door) during the test trial. After each participant's fifth search (and while still blindfolded), each participant was asked to point to the door of the experimental room. This assessed whether participants had been updating their current location with respect to this environmental feature external to the landmark array. An ability to update current location with respect to the door of the experimental room would indicate that participants were not disoriented during the test trial (and hence choices during testing may have been based upon this spatial cue instead of that of the landmark array). However, an inability to update current location with respect to the door of the experimental room would provide evidence that participants were disoriented (or at least not oriented with respect to the only conspicuous feature of the experimental room – the door). Such an inability to update current position with respect to the door of the experimental room would rule out the use of the experimental room door as a possible source for choices during testing). Pointing responses were coded such that pointing within  $\sim 22.5$  deg to either side (i.e. a 45 deg total) of the center of the experimental room door was considered correct. All others were considered incorrect. (Ideally, we would have recorded the precise angular deviations of pointing responses from the experimental room door to allow for the use of circular statistics. The use of circular statistics would have allowed determination of

whether participants were statistically oriented to some other potential feature of the experimental room.)

## RESULTS

### Training

All participants met the training criterion of five consecutive corrective first choices and learned to use their distinctive textural cue to locate the wooden block (trials to reach criterion,  $8.17 \pm 0.49$ ; mean  $\pm$  s.e.m.). To investigate the time course of learning, we analysed the extent to which first choice was correct for the first four trials of training (trials that allowed for the inclusion of all participants) by creating two, two-trial blocks. A two-way mixed analysis of variance (ANOVA) on mean proportion of correct first choices with 'gender' (male, female) and 'block' (1–2) as factors revealed only a main effect of block ( $F_{1,22}=15.96$ ,  $P<0.001$ ). Neither the effect of gender nor the interaction was significant ( $F_s<3.98$ ,  $P_s>0.05$ ). A least-significant differences (LSD) *post hoc* test on the block factor revealed that the mean proportion of correct first choices for Block 2 ( $0.67 \pm 0.08$ ; mean  $\pm$  s.e.m.) was significantly greater ( $P<0.01$ ) than that of Block 1 ( $0.31 \pm 0.07$ ; mean  $\pm$  s.e.m.). In addition, the mean proportion of correct first choices for Block 1 was not significantly different from chance (i.e. 0.25; one-sample *t*-test,  $t_{23}=0.95$ ,  $P=0.35$ ), but was significantly greater than chance for Block 2 (one-sample *t*-test,  $t_{23}=5.0$ ,  $P<0.001$ ). These results suggest that participants rapidly learned (i.e. within the first four trials) to utilize their respective distinctive textural cue to determine the correct location at above-chance levels.

### Testing

For testing, we analysed the allocation of choices to the four locations. Consistent with previous research (Cheng and Newcombe, 2005), locations were defined as to whether they were (1) correct (where rewarded texture would have been), (2) near (the geometrically incorrect location closest to the correct location), (3) far (the geometrically incorrect location furthest from the correct location), and (4) rotational equivalent (the 180 deg equivalent of the correct location). Choices were transformed for data presentation purposes to be as if the rewarded (i.e. trained) location was located at the top left location shown in Fig. 2 for all participants (even though the rewarded location was counterbalanced across participants – see Materials and methods). Fig. 2 shows the allocation of the proportion of participants' first choices (left panel) and mean proportion of participants' first three choices (right panel) during testing in the absence of the distinctive textural cues.

#### First choice

As a measure of initial choice, we analyzed participants' first choice (Fig. 2, left). Importantly, the proportion of first choices to the correct and the rotational equivalent locations were not significantly different from each other (binomial test,  $z=-0.58$ ,  $P=0.56$ ), and the total proportion of first choices (i.e. 0.92) to these geometrically correct locations was significantly above chance [i.e.  $0.5$ ;  $\chi^2(1, N=24)=16.67$ ,  $P<0.001$ ]. This suggests that in the absence of the distinctive textural cues, participants were able to utilize the geometric properties of the landmark array to immediately guide their search behavior. However, they were unable to disambiguate the correct from the rotationally equivalent location (i.e. demonstrated the rotational error phenomenon).

#### Mean proportion of first three choices

Due to experimenter error, two male participants were only allowed four searches during testing (instead of the predetermined five total

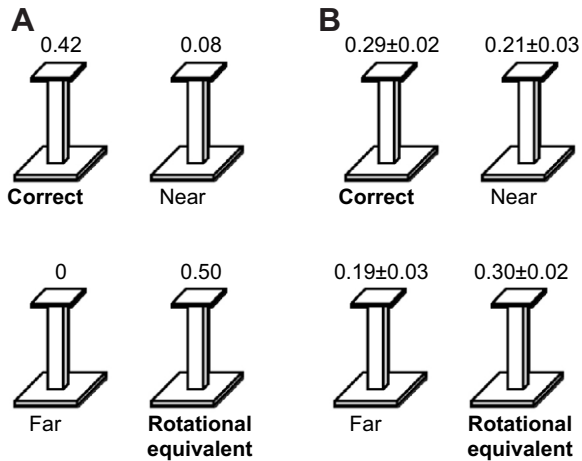


Fig. 2. (A) Allocation of the proportion of first choices ( $N=24$ ) to each location during testing. (B) Allocation of the mean proportion of first three choices during testing. Please note that choices were transformed for data presentation purposes to be as if the rewarded (i.e. trained) location was located at the top left location for all participants even though the rewarded location was counterbalanced across participants (see text for details). 'Correct' and 'Rotational equivalent' locations are labelled in bold to illustrate the geometrically correct locations. '±' denotes plus or minus standard errors of the means.

searches). Because there were no repeats within the first four searches for any participant, an odd number of searches was required to assess differences in the allocation of choices. As a result, we selected the first three choices. As shown in Fig. 2 (right panel), the mean proportion of first three choices also did not differ between the correct and rotationally equivalent locations. This was confirmed with a two-way mixed ANOVA on mean proportion of first three choices with gender (male, female) and location type (correct, rotational equivalent) as factors that revealed no main effects or interaction ( $F_s < 0.24$ ,  $P_s > 0.63$ ). Importantly, as with first choice, the total mean proportion of first three choices ( $0.59 \pm 0.03$ ; mean  $\pm$  s.e.m.) to these geometrically correct locations (i.e. correct and rotationally equivalent locations) were significantly greater than chance (i.e. 0.50; one-sample  $t$ -test,  $t_{23} = 3.27$ ,  $P < 0.01$ ). Consistent with first choice, the mean proportion of first three choices suggests that in the absence of the distinctive textural cues, participants were able to utilize the geometric properties of the landmark array to guide their search behavior. Also consistent with first choice, participants were unable to disambiguate the correct from the rotationally equivalent location (i.e. demonstrated the rotational error phenomenon).

#### Mean proportion of all choices

It should be noted that the allocation of the mean proportion of all five choices for the 22 participants that were allowed five searches during testing was consistent with both first choice and mean proportion of first three choices reported above. Specifically, the mean proportion of choices to the correct and rotational equivalent locations did not differ from each other, paired-samples  $t$ -test ( $t_{21} = 1.23$ ,  $P = 0.23$ ), but the mean proportion of choices allocated to these geometrically correct locations ( $0.57 \pm 0.02$ ; mean  $\pm$  s.e.m.) was significantly greater than chance (i.e. 0.5; one-sample  $t$ -test,  $t_{21} = 3.78$ ,  $P < 0.01$ ). [Due to an uneven number of males and females (because of the removal of the two males that were mistakenly not allowed to make five choices during testing), we did not analyze gender as a factor (i.e. we collapsed across gender). As a result, a

paired samples  $t$ -test (instead of an ANOVA) was conducted to compare correct and rotational equivalent locations.] In addition, the fifth choices (i.e. the only revisit to a previously searched location) to the correct (0.32) and rotationally equivalent (0.45) location were not significantly different from each other (binomial test,  $z = -0.94$ ,  $P = 0.35$ ), and the total proportion of this fifth choice (i.e. 0.77) to these geometrically correct locations was significantly above chance [i.e. 0.5;  $\chi^2(1, N=22) = 6.55$ ,  $P < 0.05$ ].

#### Confirmation of attempt to disorient

Although equivalent response to the trained and rotational equivalent location provide evidence that participants were disoriented with respect to the experimental room as well as the landmark array, we attempted to provide additional evidence by analyzing the proportion of participants' pointing responses that were allocated to the experimental room door. Only two participants (i.e. 8%) were able to accurately point to the location of the experimental room door following testing. Given that the pointing responses were coded as correct (i.e. pointed to the experimental room door) or incorrect (pointed elsewhere), we utilized a  $\chi^2$  test to determine whether this value significantly differed from that which would be expected on the basis of chance (45 deg/360 deg = 13%). The result was not significantly different than would be expected on the basis of chance [ $\chi^2(1, N=24) = 0.38$ ,  $P = 0.53$ ]. This suggests that participants could not point to the location of the experimental room door any better than chance. This result coupled with the inability to differentiate the correct from the rotationally equivalent location (either for first choice or mean proportion of choices) provides converging evidence that participants were disoriented with respect to the experimental room during testing (or at least were unable to update current position with respect to the only conspicuous feature in the experimental room). Collectively, these results suggest that participants were relying on the geometric information provided via the landmark array for orientation.

#### DISCUSSION

Training results suggest that disoriented and blindfolded adult human participants were able to learn to use a distinctive textural cue to determine a target object. Importantly, this textural cue was both necessary and sufficient during training to successfully determine the target object. Despite array geometry being neither necessary nor sufficient to determine the target object during training, testing results revealed that the disoriented and blindfolded adult human participants learned about this geometric information. Specifically, in the absence of the unique textural cues, participants allocated their choices to the correct and rotational equivalent locations (i.e. geometrically correct locations) at above-chance levels. Such a result could only occur had participants incidentally learned the geometry of the landmark array during training.

As such, our results suggest that participants incidentally learned the geometry of the landmark array during training and are the first to suggest that the rotational error phenomenon is not constrained to the visual modality. It should be noted that although the magnitude of choices to the correct and rotationally equivalent locations was relatively large for first-choice performance (i.e. 0.92) – consistent with prior experiments *via* vision, the magnitude of this effect diminished when averaged over the first three choices (i.e. 0.59) and when averaged over all five choices (i.e. 0.57) – appearing smaller *via* touch compared with that of previous experiments *via* vision (for a review, see Cheng and Newcombe, 2005). Although this smaller magnitude may be related to a greater error in learning distances for touch compared with vision [i.e. overestimations *versus*

underestimations, respectively (Lederman and Taylor, 1969)], we believe that this diminished magnitude of the effect is an artifact resulting from the relatively low maximum possible values that could be allocated to these two locations given that there were no revisits in the first three choices (i.e. resulting in a maximum possible value of 0.67: two out of three) and only one revisit with all five choices (i.e. resulting in a maximum possible value of 0.60: three out of five).

Regardless of the potential reason(s) for the smaller magnitude when averaged across choices, both the mean proportion of first three choices and the mean proportion of all choices to the geometrically equivalent locations were above chance levels, and we believe our paradigm provides a method for the continued exploration of the extent to which various phenomena associated with the incidental visual learning of environmental geometry hold via touch. Such a protocol allows for the continued exploration of the similarities and differences in the mechanisms underlying visual and haptic spatial learning and serves as an impetus for future exploration of cross-modal transfer in the spatial domain.

We believe that these results for the incidental learning of landmark array geometry in the absence of vision provide the first demonstration that environmental geometry is capable of being both learned and manifested in a non-visual modality in adult humans. Perhaps more importantly, such an interpretation of incidental learning of array geometry *via* touch rules out the possibility of the use of a strict view-based matching strategy (Cheng, 2008) because search performance was constrained to the correct and rotationally equivalent locations despite the absence of visual input during training and testing. This means that encoding a visual memory (during training), accessing current visual perception (either in training or testing), and reducing discrepancy between current visual perception and a stored visual memory (during testing) was prohibited. It is worth noting that under a strict definition of view-based matching (i.e. requiring visual input), learning of the array geometry in the present task would have been prohibited due to a lack of visual input; however, we acknowledge that a more liberal interpretation of view-based matching may suggest that the content of the stored 'views' could occur *via* other sensory modalities other than vision as long as they occur in an egocentric (as opposed to an allocentric) frame of reference (Wystrach and Graham, 2012).

We acknowledge that the size of the landmark array used in the present experiment was of a relatively small scale. Given the dimension of the array, participants had all landmarks relatively close to the starting position in each trial. Because we neither explicitly instructed participants to use one hand nor explicitly recorded whether participants were exploring the response locations with one or both hands, we acknowledge the possibility that the geometrically correct landmarks could have been learned based upon different proprioceptive feedback provided by the arms exploring pairs of landmarks simultaneously. Although we estimate that only approximately five out of 24 (~21%) of participants used two hands during the haptic task, it remains possible that some participants associated a left or right response based upon the pair of landmarks being explored. Thus we acknowledge that some participants might have relied on an egocentric local strategy to respond to both the correct and rotationally equivalent locations.

Whether or not our results would be obtained with landmark arrays of a much larger scale remains an open question, but our results appear consistent with explanations of orientation related to the fundamental and incidental learning of the geometric properties of the environment (Cheng, 1986; Gallistel, 1990; Sturz et al., 2011b). Present results can be incorporated into existing models of

orientation by including haptic input as a means by which geometric information is learned and haptic output as a means by which this learning of geometric properties is revealed (Cheng, 1986; Gallistel, 1990; Newcombe and Ratliff, 2007; Bodily et al., 2011; Lee and Spelke, 2011; Sturz et al., 2011b; Lee et al., 2012). Importantly, the mechanism(s) producing the behavioral output in adult humans appear to not rely on a process of matching stored views to current visual perception.

## ACKNOWLEDGEMENTS

We would like to thank Rachel Geary and Jessica Valdez for assistance with data collection. We thank Kent D. Bodily for comments. We are grateful to three anonymous reviewers for their helpful suggestions on a previous version of the manuscript.

## FUNDING

This research was supported in part by funds from the Office of the Vice President of Research and the Jack N. Averitt College of Graduate Studies at Georgia Southern University to B.R.S.

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