

BRIEF COMMUNICATION

Of Mice (*Mus musculus*) and Toddlers (*Homo sapiens*): Evidence for Species-General Spatial Reorientation

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There is ongoing debate in spatial cognition about the mechanisms by which organisms are able to reorient, or reestablish a position, in the world after losing their bearing. The traditional view is that there is an encapsulated reorientation module that can only process environmental geometry such as distances or angles (Cheng, 1986). Recently, this view has been challenged on the grounds that the reorientation mechanism is only able to accept geometric information and may instead depend on a more general ability to use relative cues. J. Huttenlocher and S. F. Lourenco (2007) demonstrated that toddlers are successfully able to reorient with continuous cues but show remarkable deficits using categorical cues that are similar in perceptual complexity for reorientation. Here, the authors show the same pattern of results with mice (*Mus musculus*). These findings provide evidence that there is a homologous reorientation mechanism between mice and humans. Thus, future researchers can examine the genetic basis of this important cognitive ability.

Keywords: reorientation, geometric module, spatial cognition, adaptive combination, genetics

For all mobile organisms, maintaining orientation is a critically important skill, especially for finding resources such as food, shelter, or social groups. It has been widely demonstrated that various species can reorient on the basis of the geometric information in the environment, such as relative wall length or corner angle. It is important to note that rats in working memory tasks and human children (but not human adults) often ignore relevant feature information—such as colored walls or odor cues—that could have enabled complete reorientation (Cheng, 1986; Hermer & Spelke, 1994, 1996).

To explain this somewhat surprising pattern of results, Cheng (1986) proposed that reorientation was primarily achieved on the basis of geometric information, and feature information could then be pasted onto this geometric reference frame. This was the original geometric module proposal. Even though geometric information did not allow for perfect search in the experiment, it was argued to be more stable than features in the natural environment which can change—from season to season, for example. For people, mastery of the spatial terms *left* and *right* has been claimed to predict use of nongeometric information. Thus, a geometric module-plus-language

hypothesis was put forth as one explanation for how adults are able to flexibly combine feature and geometric information (Hermer-Vazquez, Moffet, & Munkholm, 2001; Hermer-Vazquez, Spelke, & Katnelson, 1999).

Recently, this module-plus-language position has come under attack. First, many nonlinguistic species are readily able to use feature information (Cheng & Newcombe, 2005). Second, children who have not yet mastered *left* or *right* are able to flexibly combine feature and geometric information with only a very small amount of practice, with functionally relevant features, or when in larger spaces (Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, & Huttenlocher, 2001; Twyman, Friedman, & Spetch, 2007). Third, language does not appear to be necessary for adults to use features (Ratcliff & Newcombe, 2008).

Most recently, the specificity of the geometric module has been questioned. Toddlers were asked to search for a desirable object in a square enclosure lacking unique geometric information. Toddlers were successfully able to reorient using information on the walls that varied along a continuum (large and small circles). Thus, there is some cause to doubt that the reorientation mechanism is limited only to geometric information (Huttenlocher & Lourenco, 2007). Instead, reorientation may be supported by a general ability to use relative cues (including geometry) more readily than nonrelative cues (e.g., distinct colors or odors). In the case of adjacent walls with small and large dots, relative cues such as size, number, or density could have been used for reorientation. When the adjacent walls were not related along a continuum, for example, yellow versus blue or gray versus polka dot, toddlers failed to reorient (Huttenlocher & Lourenco, 2007).

It is possible that an aspect of human cognition, such as symbolic ability or early language, may have enabled toddlers to succeed where other species would fail. Thus, we tested the ability of nonhuman animals to reorient using relative information. By comparing and

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contrasting the cognitive abilities of human and nonhuman animals, it is possible to identify where animal models can be used to study the neurological underpinnings of cognition and where it might be best to use alternative methods, a point raised and a general research strategy used by Penney, Gibbon, and Meck (2008). Additionally, if the reorientation mechanism appears to be shared across species, then this mouse model will facilitate an investigation of the genetic foundation of spatial cognition.

Experiment 1

To the best of our knowledge, mice have not previously been tested for their reorientation ability in the food reinforcement paradigm. In a water maze version of the task, adult male mice successfully used both geometric and feature information (Fellini, Schachner & Morellini, 2006). To establish the comparability of mice to other species, mice were trained to find a chocolate pellet in the corner of a continuous uniform rectangular search space.

Method

Five experimentally naïve mature male C57BL/6 mice (*Mus musculus*) participated in this experiment. The mice were housed in groups of 2 to 4 in a standard animal care facility on a 12-hr light–dark cycle from 7 a.m. to 7 p.m. To increase motivation to participate in the task, the animals were maintained at 85%–90% of their free-feed weight.

The search space was a uniform white rectangle $19.7 \times 29.2 \times 8$ cm. On each trial, the apparatus was randomly rotated 90° , 180° , or 270° . Mice were transferred from their home cage to an 8.9-diameter \times 11.4-cm-high cylinder. To disorient the mice, the experimenter turned the cylinder four complete revolutions to the right and then to the left. The container was placed on its side facing a randomized wall, and mice were allowed to exit the container at their leisure. Once the mice had exited the container, the mouse had 3 min to find the chocolate pellet or the trial was terminated.

To introduce mice to the new odor and flavor of the chocolate pellets (45 mg Sucrose Reward Tablet, TestDiet, Richmond, IN), once a day a centrally placed stash of 10–15 chocolate pellets was left in the home cage during this pretraining phase. By the 3rd day, the mice eagerly ate the chocolate pellets. On the 4th day, mice moved from pretraining to shaping. Over the 7 shaping days, mice were introduced to the experimental arena. The chocolate pellet was at first fully exposed at the correct corner of the uniform search space and then was gradually buried under the bedding material. The number of trials per day also increased during this shaping period. On Day 4 (the first day of training in the experimental arena), mice were given only one trial a day. This was increased to two trials on Day 5, three trials on Day 9, and finally four trials from Day 11 onward. Moving from shaping trials to training trials on Day 11, an odor mask of 10 ground chocolate pellets was mixed in with the bedding material. Once the mice were 75% correct on their first choice of four trials per day for 3 days in a row, the mice were deemed to have learned the task. After the mice demonstrated that they had learned the task, they were administered 4 days of follow-up probe trials. On each day, two probe trials were interspersed with regular training trials: on Trials 2 and 3 for Test Days 1 and 4, on Trials 1 and 3 for Test Day 2, and on Trials 1 and 2 for Test Day 3. For the probe trials, no chocolate pellets were hidden at the target corner. As soon as the mouse made the first

digging motion, with one paw, two paws, or the nose, this counted as the first choice. The search had to be within 60 cm to the left and right of the corner to count as a choice of that corner. This judgment was made in real time by one observer who was naïve to the experimental hypothesis. All values are reported as $M \pm SEM$.

Results

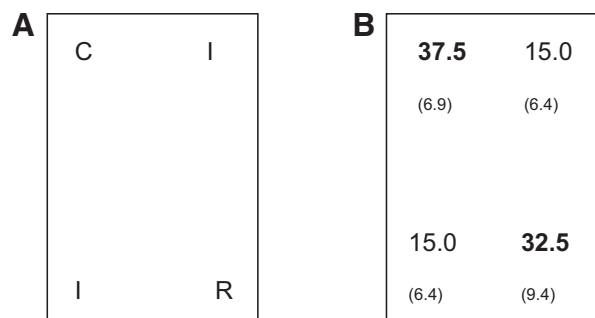
Mice reached the training criterion for the task in an average of 15.6 trials. The choices for the eight follow-up probe trials were averaged across all mice and are presented in Figure 1. As can be seen from this figure, mice were successfully able to use geometric information for reorientation. On these probe trials, the mice were able to focus their search at the correct or equivalent corner ($M = 70.0 \pm 8.2$), $t(4) = 3.14$, $p = .035$, $d = 1.40$. Thus, mice share the ability to use geometric information for reorientation with all of the previously tested species.

Experiment 2

Experiment 1 demonstrated that mice are comparable to previously studied species. It is now appropriate to compare the reorientation abilities of mice and toddlers. Here we ask whether mice are able to successfully reorient in the absence of unique geometric information and in the presence of either relative or nonrelative cues. We modified the categorical cues from Huttenlocher and Lourenco (2007), whose toddlers were presented with blue and red walls. Mice are unable to see red, so we modified the colors to blue and yellow because mice are able to perceive these colors (Haverkamp et al., 2005; Jacobs, Williams, & Fenwick, 2004). Additionally, the mice have sufficient acuity to be able to resolve the polka dot pattern (Brown & Wong, 2007).

Method

Seven female and 5 male naïve C57BL/6 mice were randomly assigned to three groups, as displayed in Figure 2. The housing conditions



Schematic of the enclosure Proportion of Responses

Figure 1. Reorientation in rectangular search spaces. A: The mice searched in a continuous space. The correct location, C, contained a chocolate pellet buried under odor-masked bedding material. On the basis of the information provided to the mouse, reorientation could only be accomplished with geometric information. For example, the mouse could have remembered to search at the corner where a long wall was on the left and a short wall was on the right. In this case, the rotationally equivalent corner, R, was counted as a correct first choice. The two other corners, I, were incorrect responses. B: First-choice responses averaged across eight probe trials from each of 5 experimentally naïve male mice, with the standard errors in parentheses.

follow that of Experiment 1. The mice that did not learn the task within 105 trials (1 additional female in each group) were omitted.

Each square enclosure had a floor area of 400 cm², covered with bedding material, and was 20 cm high. The discrete hiding location in each corner was a 3.8-cm-diameter tea candle holder. Combined with bedding material, two ground chocolate pellets (45 mg Sucrose Reward Tablet, TestDiet) were added to each holder as an odor mask. On each trial, the apparatus was randomly rotated 90°, 180°, or 270°.

Pretraining followed that of Experiment 1. For the next 7 trials, one feeder at the correct corner displayed a fully exposed reward. In the next 11 trials, the pellet was gradually buried with one feeder. In the next 15 trials, the pellet was fully buried, and all feeders were present. Last, the odor mask was added, and from this point on, we recorded how many additional days it took the mice to learn the task. Once the mice were 75% correct on their first choice of four trials per day for 3 days in a row, we were confident that the mice had learned the task, and testing began. The testing sessions consisted of a mix of the standard training trials and probe trials in which each of the hiding locations contained a mask, but no reward. A total of eight probe trials were collected over 5 days, alternating between probe trials on Trials 1 and 3 for the first test day and then Trial 2 for the next day. The probe trial choice was recorded in real time by an observer who was naïve to the experimental hypothesis. All values are reported as $M \pm SEM$.

Results

Disoriented mice searched for hidden chocolate pellets in the corners of square spaces. The three conditions, nonrelative color (yellow–blue), nonrelative pattern (dots–gray), and relative pattern (small dots–large dots), are displayed in Figure 2. For the dots–gray group, the mice were evenly divided between large dot–gray or small dot–gray enclosures. Because there were no significant differences between these groups ($M_{\text{difference}} = 6.0 \pm 15.6$), $t(2) = 0.75$, $p = .75$), the mice were combined to make the dots–gray group. Analyses across the groups revealed that there were no corner, $F(1, 8) < 1$, $p = .957$; sex, $F(1, 8) = 2.575$, $p = .147$; or Corner \times Sex interaction effects, $F(1, 8) < 1$, $p = .789$. Our disorientation procedure and removal of external cues was effective because responses at the two equivalent correct corners were evenly distributed across the correct (48%) and the rotationally equivalent corner (52%).

All of the groups were eventually able to reorient in the absence of geometric information. However, there was a large difference in the time course of acquisition across groups. Every mouse in the small–

large condition learned the task in the minimum number of trials (12). This was significantly faster than mice in either the yellow–blue group ($M = 38.0 \pm 6.5$ trials), $t(6) = 4.50$, $p = .004$, $d = 4.50$, or the dots–gray group ($M = 33.0 \pm 6.7$ trials), $t(6) = 3.09$, $p = .022$, $d = 3.09$. There were no significant differences between the yellow–blue and the dots–gray groups on task acquisition, $t(6) = 0.56$, $p = .60$, $d = 0.08$.

Because we collected eight probe trials, it is possible to compare accuracy and variability on these probe trials for the mice with those of the toddlers from Huttenlocher and Lourenco (2007). The toddlers accurately searched at the equivalent corners about $70 \pm 5\%$ of the time. The mice performed similarly. The mice in the small–large group were $80 \pm 11\%$ accurate. The mice in the yellow–blue and dots–gray groups were $69 \pm 6\%$ and $69 \pm 8\%$ accurate, respectively. These groups did not significantly differ from each other on accuracy, $F(2, 9) = 1.50$, $p = .27$, which is perhaps not surprising because all of the mice had to pass the same accuracy threshold to move from training to the follow-up probe trial tests.

Discussion

Our study demonstrates a striking parallel between the reorientation abilities of mice and toddlers. Mice, similar to many other species, are able to use geometric information when it is available. Just like toddlers, mice are also able to reorient in the absence of geometric information when nongeometric information is present. When information varies along a single dimension, both mice and toddlers readily reorient. However, introducing nonrelative cues makes reorientation considerably more difficult for both mice and toddlers. This experiment provides evidence that the reorientation mechanism, regardless if it is encapsulated or not, is readily able to use both geometric and relative, nongeometric information for reorientation.

In addition, our data warrant a more nuanced view of the use of relative versus categorical cues. Through the many trials collected with the animal model, in contrast to the limited trials with children, we showed that the colored walls could eventually be used for reorientation, although this was far more difficult to learn. Recent work with toddlers hints at the same conclusion. Two studies have examined toddlers in square enclosures, with adjacent walls in different colors and opposite walls of the same color, where chance is 50% because two of the corners are identical (i.e., blue on the left and yellow on the right). In one study with adjacent walls of red and blue, toddlers searched at the correct corner 44% of the time, not significantly different from chance (Huttenlocher & Lourenco, 2007). How-



Figure 2. Training chambers for Experiment 2. All of the square boxes were of equal size. The proportion of black and white paint was identical for each wall in Groups a and c.

ever, with adjacent walls of blue and white, a larger search space, and two additional trials, toddlers were able to (weakly) use a categorical cue to focus search about 60% of the time at a correct corner (Nardini, Atkinson, & Burgess, 2008).

Thus, overall, it appears that categorical information as well as relative cues can be used to reorient, but more learning is required for this to be possible. An adaptive combination approach to reorientation argues that any possible source of information can be encoded and then stored in an integrative manner and used for reorientation (Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). Thus, adaptive combination predicts that all three groups will learn the task. The particular information used at a given point in time will depend on its relative salience and past history of success. Thus, there are many reasons for this position to predict that the small–large comparison will be acquired the fastest. The small–large comparison has two relative dimensions because the walls vary both in dot size and in the number of dots per wall. Additionally, because ordinal information may be more readily mapped onto spatial position than nominal information, the adaptive combination approach predicts that all three groups will learn, but that the ordinal (small–large) comparison will be learned the fastest, as we found.

Two more recent models of spatial reorientation do not fit these data. First, the operant version of the Rescorla–Wagner model, given the current parameters, does not make differential predictions for our groups and as a result does not account for our data (Rescorla & Wagner, 1972). Second, local view theory suggests that the subject moves in the direction that increases the match between the current view and the stored retinal image of the correct location (Cheung, Sturzl, Zeil, & Cheng, 2008; Sturzl, Cheung, Cheng, & Zeil, 2008). Our data are also problematic for this account, again because it suggests that all three conditions should be of equal difficulty.

In summary, our data are problematic for the specificity of the geometric module, the current version of the operant Rescorla–Wagner model, and the local view hypothesis. Our data support adaptive combination theory, an aspect of which is the greater ease of using relative over categorical cues. However, aspects of the other models may be needed for a complete account of spatial reorientation.

Perhaps the most exciting implications of this study is that the reorientation mechanisms of mice and people appear to be homologous. Thus, the mouse model can be used to examine the genetic foundation of this important cognitive ability.

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