

Four-Dimensional Spatial Reasoning in Humans

T. N. Aflalo and M. S. A. Graziano
Princeton University

Human subjects practiced navigation in a virtual, computer-generated maze that contained 4 spatial dimensions rather than the usual 3. The subjects were able to learn the spatial geometry of the 4-dimensional maze as measured by their ability to perform path integration, a standard test of spatial ability. They were able to travel down a winding corridor to its end and then point back accurately toward the occluded origin. One interpretation is that the brain substrate for spatial navigation is not a built-in map of the 3-dimensional world. Instead it may be better described as a set of general rules for manipulating spatial information that can be applied with practice to a diversity of spatial frameworks.

Keywords: spatial processing, path integration, spatial adaptation, mental rotation, maze learning

The world in which we live contains three spatial dimensions. Humans are able to navigate successfully within these dimensions through mazelike environments of roads and building corridors. We remember routes, take spatially correct shortcuts, and plot return paths. Some of these spatial abilities have also been demonstrated in rats, bees, and ants (Gould, 1986; Menzel, Geiger, Joerges, Muller, & Chittka, 1998; Muller & Wehner, 1988; Tolman, 1948).

The classic test for spatial geometric ability is a shortcut test. Tolman (1948) tested whether rats learned their way through a maze by the use of nonspatial stimulus–response associations or instead by the use of spatial cognition. First, a rat learned a maze to competency. Then the rat was tested with a version of the maze in which a shortcut could be taken to the goal. Tolman argued that if the rat used spatial cognition, it would know to take the shortcut. The results suggested that rats had some capacity to take the shortcut and therefore had some ability for spatial cognition. Shortcutting has also been used to probe the spatial ability of bees and ants (Gould, 1986; Menzel et al., 1998; Muller & Wehner, 1988). Desert ants in particular make good navigators, foraging for food meters from the home nest along winding routes and then returning to home along a straight path (Muller & Wehner, 1988).

Shortcutting is a test of navigational path integration (Biegler, 2000; Collett & Collett, 2002; Newcombe & Huttenlochner, 2000; Wehner, Michel, & Antonsen, 1996). Path integration is the ability to follow a winding path and mentally sum the lengths and turns, keeping track of the spatial relationships between start point, via points, and end point. Animals that can perform path integration have true geometric expertise. Some controversy has arisen, however, over whether shortcutting implies the presence of a cognitive map (Bennett, 1996; Gallistel, 1990; O’Keefe & Nadel, 1978).

Even the existence of cognitive maps in humans has been questioned (Bennett, 1996). Whereas it is clear that shortcutting implies path integration and therefore spatial expertise, the exact type of spatial mechanism, whether best described as an internal map of the world or as a set of propositional rules for handling spatial relationships, is not clear and may depend on the species of animal.

In humans, the ability to perform mental spatial rotation has long been established (Shepard & Metzler, 1971). Whether this ability to perform mental rotation underlies the human ability to keep track of the locations of objects in the environment has been debated (e.g. Hintzman, O’Dell, & Arndt, 1981). Humans are able to perform path integration, keeping track of distances and angles as they traverse a path (Easton & Sholl, 1995; Farrell & Thomson, 1998; May & Klatzky, 2000; Presson & Montello, 1994). Much of this work on path integration has focused on nonvisual cues, tested in subjects who are blindfolded, but humans can also perform spatial updating purely on the basis of visual cues, such as in virtual, computer-generated environments (Riecke, Cunningham, & Bultoff, 2007; Wraga, Creem-Regehr, & Proffitt, 2004). The neural mechanisms for spatial updating, mental rotation, and spatial navigation are believed to be emphasized in the hippocampus and the right parietal lobe (e.g., Farrell & Robertson, 2000; O’Keefe & Nadel, 1978).

Like all animals, humans evolved in and gained developmental experience in a world that contains three euclidean spatial dimensions. One possibility is that the neural machinery for spatial navigation is narrowly specialized to encode the geometric topology of the real world, plotting positions, angles, and routes in three-dimensional (3-D) euclidean space. In this hypothesis, the brain basis for spatial navigating and spatial updating is tailored to the constraints of a 3-D world. A topologically different world, such as a 4-D world, would be fundamentally impossible for this machinery to process. A second possibility is that the neural machinery is more flexible, adept at general rules and operations useful in geometric reasoning such as encoding distance relationships and performing coordinate rotations. In this hypothesis, the neural machinery for spatial navigation would, with practice, be able to encode and navigate a world that is topologically different from the real world.

T. N. Aflalo and M. S. A. Graziano, Department of Psychology, Princeton University.

This research was supported by National Institutes of Health Grant NS-046407 to M. S. A. Graziano.

Correspondence concerning this article should be addressed to M. S. A. Graziano, Department of Psychology, Green Hall, Princeton University, Princeton, NJ 08544. E-mail: graziano@princeton.edu

Although most people presumably cannot imagine a 4-D world, it is possible to describe a 4-D world mathematically. A 4-D topology follows the same geometric rules as a 3-D topology but has one added basis vector orthogonal to and otherwise equivalent to the three familiar spatial basis vectors. It is possible to create a computer simulation of how a 4-D world would look if viewed by a human with a normal 2-D retina. In a 4-D topology, just as in the 3-D case, light rays travel in straight lines, and therefore it is possible to calculate how light rays emanating from objects would project onto a 2-D computer screen. We constructed a 4-D virtual maze and displayed it in perspective on a computer screen. The display was as if the subjects were looking through a window into a 4-D environment through which the subject could navigate using a set of specified computer keys. If human subjects are able to learn to navigate through the 4-D world, such a result would indicate that spatial navigation does not rely on a rigidly built-in neural map of 3-D space but instead depends on a mechanism adept at the underlying operations of spatial relationships.

Some hints exist that humans can adapt to and learn to operate within an imagined or virtual 4-D world. Mathematicians sometimes claim to be able to think geometrically within 4-D. After practice with computer simulations, gamers claim to develop competence in 4-D (Seyranian, Colantoni, & D'Zmura, 1999). These hints, however, are often anecdotal and based on subjective report. Moreover, even the ability to solve a specific task within a 4-D world does not itself imply 4-D geometric reasoning. Other strategies could in principle be used to operate within a 4-D environment, such as the use of 3-D intuition to partially solve the problem or the use of local stimulus features to guide a set of memorized responses. The present experiment required a rigorous measure of spatial ability that could show whether human subjects developed true 4-D navigational skills. We used path integration as an assay of navigational spatial ability because, as reviewed above, path integration has been extensively studied and successful path integration unambiguously requires spatial expertise. Using a computer-generated video-game-like environment, subjects navigated through a virtual corridor displayed on a computer screen, following a set of turns to the end of the corridor, and then attempted to point in a straight line toward the no-longer-visible entrance. We tested the subjects' ability to perform this path integration task in 2-D, 3-D, and 4-D virtual environments.

Method

Subjects

All procedures were approved by the Princeton University institutional review board. Five adult subjects (4 male, 1 female) participated. Subjects navigated three types of computer-generated virtual mazes: 2-D, 3-D, and 4-D. One potential difficulty with the experiment was that 4-D reasoning might be so difficult to acquire, or require so much practice, that it might not be demonstrable within a few hours of practice in the lab. To circumvent this potential problem and to ensure the subjects had an effectively unlimited amount of practice time, the subjects were allowed to play the game on their own computers on their own time. Subjects were questioned first to ensure that they had the correct computer hardware to support the program. Most standard home and office computers purchased after 2004 were sufficient, allowing the

program to create similar display sizes, colors, resolution, and navigational movement speed. All subjects in the study had the requisite computer equipment.

Subjects were provided with the maze display program to load onto their home or work computer, along with an instruction document that described the task and the keystrokes needed to navigate through the mazes. When the program was opened it first displayed a menu allowing the subject to choose a 2-D, 3-D, or 4-D maze. Subjects were free to attempt a 2-D, 3-D, or 4-D maze at any time. The program was equipped with a library containing 100 different examples of each type of maze. On each trial, the subject chose a type of maze, and the program randomly selected a specific maze from the set of 100 possible examples of that maze type (using selection with replacement). The program automatically stored the type of maze, the date and time of playing, the amount of time spent within the maze, and the angular accuracy (described below) of the subject's response at the end of the maze. The time logs indicated that subjects typically played 15 min to 1 hr a day for several weeks.

2-D mazes

In each 2-D maze, the subject was confronted with a virtual corridor. The subject saw a perspective view of the corridor (Figure 1A) displayed within a 15×15 -cm window on a standard computer screen. Features of the maze that were "in front" of the subject in the virtual world were visible in the display, whereas features that were "behind" the subject were not visible. The appearance was therefore as if the subject were looking through a 15×15 -cm window into the virtual corridor. By means of a set of keys on the standard keyboard, the subject could translate forward and backward and could rotate toward the left or toward the right, within the virtual world of the maze. In reality, of course, the subject remained still and the maze moved within the display window in the opposite direction. In Figure 1A, the corridor proceeds straight and in the distance bends to the right. To travel along the corridor, the subject would need to use the forward motion key to travel to the end of the initial segment, use the rightward rotation key to rotate toward the right until the new length of corridor was straight ahead, and then use the forward motion key again to proceed along the new length of corridor.

Also shown in Figure 1A, the corridor consisted of a series of cubes through which the subject could pass. Each cube wall was indicated by means of a purple square around the perimeter of the wall. Structuring the corridor into cubes in this way provided a visual texture on the walls that enhanced the perspective cues and optical flow cues during motion. Walls were impermeable. If the subject bumped into a wall, no more forward motion was possible unless the subject turned away from the wall. Depth was depicted in the visual display by means of standard perspective, motion parallax, and occlusion. Movement through the maze resulted in the view of the maze changing in the appropriate fashion to mimic motion through the virtual environment.

In a 2-D maze, the bends in the corridor were either to the right or to the left, and therefore the maze remained within a horizontal plane. The corridor contained three right-angle bends. The direction of each bend (right or left) varied randomly from maze to maze. The length of each straight segment of corridor varied randomly from three to six cubes, within the constraint that the

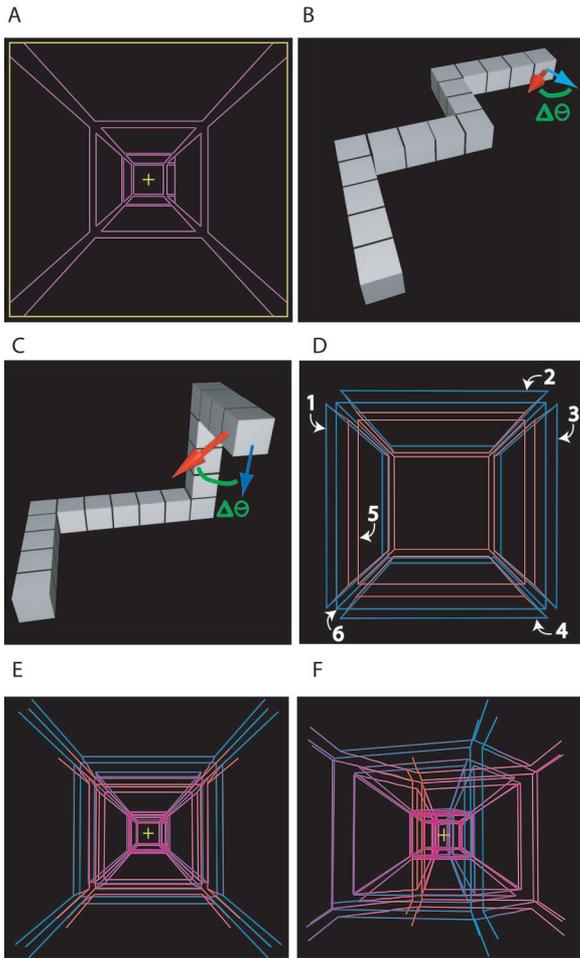


Figure 1. Three categories of mazes. A: The subject's view of a 2-D maze down a length of corridor to the first bend, in this case to the right. The yellow square shows the field of view. The yellow cross shows the center of view. The subject could translate forward or backward and rotate through all principle rotational degrees of freedom by means of keyboard controls. B: An outside view of an example 2-D maze showing the four links and three bends. The red arrow at the end shows the correct direction for the subject to point toward the origin. The blue arrow shows an example pointing choice by a subject. The angular deviation between these two arrows was used as a measure of path integration. Subjects never saw this outside view. They saw only a perspective view from inside the corridor. The start of the maze was not visible from the final box in which the subject pointed. C: An outside view of an example 3-D maze. D: One box in a 4-D maze. The full corridor is not shown. Red indicates items to the hot of the observer, and blue indicates items to the cold of the observer. This hypercube was composed of six barriers, each barrier with a cubic structure. These barriers blocked movement to the left (Cube 1), up (Cube 2), right (Cube 3), down (Cube 5), and cold (Cube 6). The hypercube was open at the front and back. E: An example of a subject's view of a 4-D maze. The corridor extends directly ahead and in the distance bends toward the right. F: The same corridor seen in E but after the subject has rotated partially in the R5 direction (see Method for an explanation of R5 rotational degree of freedom).

corridor was never allowed to intersect itself. In the cube at the beginning of the corridor, each of the five closed walls was marked with a silver square. In the final cube at the end of the corridor, each of the five closed walls was marked with a golden square. In

this way, if the subject became disoriented and returned to the start box instead of arriving at the end box, the visual cue would allow the subject to see the error, turn around, and continue trying to reach the end.

On reaching the end of the corridor the subject was prompted by the word *Point* that appeared on the visual display. The task was to point toward the start of the maze even though it was hidden behind the three occluding bends. The subject rotated within the virtual world using the navigation keys until the subject's forward line of sight, indicated by a crosshairs that was at the center of the field of view, was aimed toward the estimated direction of the start of the maze. Once the subject felt that the aim was correct, he or she pressed a key to finalize the choice and the run ended. The angular deviation between the direction to the start of the maze (the correct vector) and the direction chosen by the subject (the chosen vector) was used as a measure of spatial ability. An error of 0° corresponded to exactly accurate pointing. If a subject pointed randomly, the error could be anywhere between 0° and 180° , with an expected mean error of 90° .

Figure 1B shows an outside view of a 2-D maze with the correct pointing vector indicated in red and the subject's chosen vector indicated in blue. The angular deviation between these two vectors, $\Delta\theta$, is also indicated in the figure. The subject never saw an outside view of the maze; it is shown here only for clarity. At the end of each trial, the program displayed on the screen the angular error score for that run. This feedback after each maze was intended to allow the subject to learn through experience. In effect the subjects were able to evaluate their task strategies by monitoring their scores.

3-D Mazes

The 3-D mazes were constructed in a manner similar to the 2-D mazes. All aspects of the appearance, perspective, display size, and structure of the mazes were the same as in the 2-D case except for the direction of the bends. The corridor contained three bends (as in the 2-D case), but the bends could be in the horizontal (left or right) or vertical (up or down) direction. The directions were varied randomly from one maze to the next, within the constraint that at least one bend was in the horizontal plane and at least one bend was in the vertical plane. Figure 1C shows an outside view of a 3-D maze that had one horizontal bend followed by two vertical bends. Again, subjects never saw an outside view of the maze; they saw a perspective view from inside the maze corridor. The outside view is shown here only for clarity.

In navigating through the 3-D mazes, the subject used specified keys on the keyboard to move forward or backward and to rotate through the three principle rotational degrees of freedom: yaw, pitch, and roll. For example, consider a corridor that extends straight ahead and then bends 90° up. To traverse this corridor, a subject would be required to use the forward motion key to reach the end of the initial corridor segment. The subject would then use the upward rotation key (rotation in pitch) to turn upward, until the second corridor segment appeared straight ahead. In this new orientation, the subject essentially would be walking up the wall of the new corridor. Equivalently, one can consider the subject to have remained still and the maze to have rotated around the subject, such that the initial corridor segment was now vertically above the subject and the second corridor segment was now

directly ahead of the subject. The subject would then use the forward motion key to travel along the second corridor segment. This type of vertical rotation of the path direction was possible because, in the world of the virtual mazes, there was no gravity and therefore no intrinsic downward direction to the maze.

After passing around three bends, the subject reached the end of the corridor. As in the case of the 2-D mazes, the subject was prompted by the word *Point* that appeared on the visual display. The task was to point toward the start of the maze even though it was hidden behind the three occluding bends. The subject rotated using the navigation keys until the subject's forward line of sight, indicated by a crosshairs that was at the center of the field of view, was aimed toward the estimated direction of the start of the maze. Once the subject felt that the aim was correct, he or she pressed a key to finalize the choice and the run ended. The angular deviation between the direction to the start of the maze (the correct vector) and the direction chosen by the subject (the chosen vector) was used as a measure of spatial ability. Note that even though the mazes involved a 3-D configuration, with the corridor bending both horizontally and vertically, only one angular deviation was necessary to characterize the error score. Figure 1C shows an example of a 3-D maze with a correct vector (in red), a chosen vector (in blue), and the angular deviation between them ($\Delta\theta$). As in the 2-D maze, at the end of each trial, the program displayed on the screen the angular error score for that run. This feedback after each maze was intended to allow the subject to learn through experience.

4-D Mazes

The topology of the 4-D world and the features of its visual display are described more fully in the next section. The 4-D mazes were given the same general structure as the 2-D and 3-D mazes, in that each maze contained four straight segments of corridor and three 90° bends. In the case of the 4-D mazes, however, one bend was to the left or right, one was up or down, and one was cold or hot, where "cold" and "hot" are the arbitrary names used to designate directions in the mathematically defined fourth spatial dimension. The order of these bends varied randomly between mazes. The lengths of straight corridor segments varied randomly from three to six cubes. (As described in the next section, the "cubes" of which the corridors were composed, in the 4-D topology, are more properly described as "hypercubes.")

In the 4-D case, as in the 3-D and 2-D case, on reaching the end of the maze, the subject was prompted by the word *Point* that appeared on the visual display. The task was to point toward the start of the maze even though it was hidden behind the three occluding bends. The subject rotated using the navigation keys until the subject's forward line of sight, indicated by a crosshairs that was at the center of the field of view, was aimed toward the estimated direction of the start of the maze. Once the subject felt that the aim was correct, he or she pressed a key to finalize the choice and the run ended. The angular deviation between the direction to the start of the maze and the direction chosen by the subject was used as a measure of spatial ability. The calculation was made in the following way. A vector pointing from the subject's location at the end of the maze to the location of the start of the maze (correct vector) was defined. A vector pointing from the subject's location at the end of the maze in the direction of the

subject's chosen answer (chosen vector) was defined. These two vectors, sharing a single start point, had a single angle that characterized the deviation between them. This single angle, $\Delta\theta$, represented the error in the subject's answer. As in the 3-D and 2-D mazes, at the end of each trial, the program displayed on the screen the angular error score for that run. This feedback after each maze was intended to allow the subject to learn through experience.

4-D Environment

When a virtual 3-D world is displayed on a flat computer screen, a simple projective geometry is used. Virtual light rays are projected from points on objects in the virtual world to the flat screen, resulting in a display that captures the appearance of a 3-D world. This appearance includes perspective cues, motion parallax cues, and occlusion cues. Because of these cues, subjects are able to perceive a 3-D world through the window on the computer screen.

In a similar way, a virtual 4-D world can be projected onto a flat computer display. The computations are mathematically the same as in the 3-D case. Light rays are projected from points on objects in the virtual world to the flat screen, resulting in a display that captures the appearance of a 4-D world. The subject sees the projection of a 4-D world onto a 2-D surface. The geometrically correct projection was solved by McIntosh (2002), whose method we adapted. In principle, by looking at the 2-D display, one can reconstruct the 4-D world from motion parallax, perspective, and occlusion cues. All the necessary information is present in the visual display, but whether human subjects have the capacity to use that information to reconstruct the 4-D geometry was unknown. To aid subjects in comprehending this spatial projection, we incorporated an additional cue, a color scale. A greater degree of red hue indicated objects that were progressively more to the hot direction of the observer, a greater degree of blue hue indicated objects that were progressively more to the cold direction of the observer, and purple indicated objects that were at the same "temperature" as the observer.

It is critical to understand that the fourth dimension, though it is labeled here as "hot" and "cold" and its appearance was enhanced with red and blue hues, is merely space, just as the up-down dimension, the left-right dimension, and the forward-back dimension are space. They are all equivalent and interchangeable through rotation. Imagine a subject at the start of a corridor that extends directly ahead. If the subject rotates 90° toward the right (in the yaw rotational direction) using the specified computer key, the corridor now extends to the subject's left. It is the same corridor, with the same spatial structure, yet it is now aligned with the left-right dimension instead of the forward-back dimension. If the subject now rolls 90° in the clockwise direction, the same corridor that was extending toward the left will now appear to extend directly down, below the subject's virtual position. If the subject now rotates 90° downward (in the pitch rotational direction), the corridor will once again appear to be directly in front of the subject, aligned with the forward-back dimension. These rotations illustrate how the three dimensions in a normal space are equivalent and are interchangeable through the yaw, pitch, and roll rotations. In a similar manner, in 4-D space all four dimensions are equivalent and interchangeable through rotation.

In the 4-D topology, there are three additional rotational degrees of freedom, labeled here R4, R5, and R6. Just as pitch rotates the

forward direction of heading toward the upper or lower direction and yaw rotates the forward direction of heading toward the left or right direction, in a mathematically equivalent way R4 rotates the forward direction of heading toward the hot or cold direction. For example, consider a subject at the start of a corridor that extends directly ahead and then, in the distance, bends in the hot direction. To navigate this corridor the subject must first use the forward motion key to travel to the end of the first segment of corridor. The subject reaches an apparent dead end. To the novice in 4-D topology, the corridor appears to have no continuation. It does not bend to the right or left, up or down, and does not continue forward. To those experienced in 4-D, the corridor appears to have a bend in the hot direction. (The visual appearance of the 4-D corridor is discussed more fully in the next section.) If the subject rotates 90° in the R4 direction, the corridor segment that extended to the hot of the subject will become reoriented until it is directly in front of the subject. The subject can now use the forward motion key to travel along the new segment of corridor.

The remaining two rotational degrees of freedom, R5 and R6, are akin to a roll. For example, consider a subject at the beginning of a corridor that extends in the hot direction. Directly ahead of the subject, in the forward direction, is the wall of the corridor. If the subject rotates 90° in the R5 direction, the subject's direction of heading will not change, and therefore the subject will face the same wall as before, but the corridor segment that extended to the hot of the subject will now extend directly to the right of the subject. If the subject rotates another 90° in the R5 direction, the corridor that was to the right of the subject will now extend to the cold direction of the subject. With another 90° rotation in the R5 direction, this corridor that was to the cold of the subject will now extend to the left of the subject. With a final 90° rotation in R5, the corridor that extended to the left of the subject will be reoriented until it is once again extending to the hot of the subject.

If the subject now rotates 90° in the R6 direction, again the subject's direction of heading will not change, the subject will face the same maze wall as before, but the corridor segment that extended to the hot of the subject will now extend directly above the subject. If the subject rotates another 90° in the R6 direction, the corridor that was above the subject will now extend to the cold direction of the subject. With another 90° rotation in the R6 direction, the corridor that was to the cold of the subject will now extend below the subject. With a final 90° rotation in R6, the corridor that extended below the subject will be reoriented until it is once again extending to the hot of the subject.

Thus the subject has a range of rotational degrees of freedom for investigating and visualizing the corridor from any perspective. In this way the subject can navigate and turn corners in the virtual maze, whether the corner bends to the left or right, upward or downward, or in the hot or cold direction. These rotations are at the heart of the 4-D topology.

Maze Barriers in a 4-D Environment

To understand the 4-D mazes it is necessary to understand the geometric nature of a barrier. Consider first a flat, 2-D plane, termed Plane 1, and a hypothetical 2-D bug that can move within that plane. A barrier within the plane consists of a line segment. Imagine the bug is walled in by four line segments forming a

square. The square is termed Square 1. The bug cannot escape from Square 1 because the square entirely surrounds the bug.

Consider now the effect of elevating the bug incrementally above Plane 1 to a new plane, Plane 2. If the bug moves within Plane 2, it can pass above the barriers that existed within Plane 1. The bug is no longer trapped within Square 1. To the bug, it is as if Square 1 has vanished. To ensure that the bug is still confined, it is necessary to add a Square 2, or a set of lines within Plane 2 that forms a square around the bug. Square 2 is stacked on top of Square 1.

Consider now the effect of again elevating the bug incrementally above Plane 2, to Plane 3. Once again, to ensure that the bug is still confined, it is necessary to add a Square 3 that forms a set of barriers around the bug. Square 3 is stacked on top of Square 2, which is stacked on top of Square 1.

If this process is repeated, the result will be a set of squares, each one flat, but each stacked on the next like Lincoln Logs, to form a structure that has height. The structure is composed of four planar walls. The critical point in this example is that within Plane 1, an effective barrier for the bug is a line segment. But once the bug is allowed to travel above Plane 1 in the third dimension, a single line segment no longer suffices as a barrier. Instead, an effective barrier is a stacking of line segments forming a planar surface. Thus in 3-D space, a barrier is a surface.

The same steps can be applied to extend a 3-D barrier to a 4-D barrier. Consider first a 3-D world, and a person who lives within that world. Imagine the person is walled in by six planar surfaces, forming Cube 1. The person cannot escape from Cube 1 because if the person moves in any direction in 3-D space, whether up, down, right, left, forward, or backward, the person will encounter the walls of the cube.

Consider now adding a fourth dimension to the 3-D space and elevating the person incrementally in this fourth spatial dimension, placing the person at a hotter position than Room 1. The walls of Room 1, existing at a colder position, are no longer surrounding the person. If the person moves up, down, right, left, forward, or backward, he can pass beyond the walls of Room 1 because he is incrementally hotter than those walls. To ensure that the person is still confined, it is necessary to add a Room 2, or a set of surfaces surrounding the person at the new temperature.

Consider now the effect of elevating the person yet again to an incrementally hotter position in the fourth dimension. Once again, to ensure that the person is still confined, it is necessary to add a Room 3 surrounding the person at the new temperature.

If this process is repeated, the result will be a set of rooms, each one at a different temperature, ensuring that whatever temperature the person is elevated to, the person is still confined. An effective enclosure, in this case, is not a cube but a hypercube, or set of cubes that are stacked in the temperature dimension. Consider, for example, the wall blocking the person's forward progress. To the person, the wall appears to be a surface, with a width and height. But it is more than that. The wall is composed not of a single surface but of a set of surfaces, each one existing at a different temperature. If the person moves in temperature in the hot or cold direction, the wall is still present, blocking the person's forward motion. This barrier, therefore, has some extent in width, in height, and in temperature. It has an extent in three dimensions and is therefore not a square surface but a cube.

In the mazes used in this experiment, an ordinary corridor in 3-D, viewed head on, has surfaces to the left, right, top, and bottom and is open at the front and back (Figure 1A). A 4-D corridor, viewed head on, is different in the following ways. The left barrier is not a square surface but a cube. It extends not only from the top to the bottom of the corridor, and not only in the forward and back dimension, but also in temperature. Likewise, the barrier to the right, the upper barrier, and the lower barrier are cubes. In addition, the corridor has a cubic barrier that blocks the subject from moving far in the hot direction, and a cubic barrier that blocks the subject from moving far in the cold direction. The subject is hemmed in on the right, left, top, bottom, hot, and cold by barriers and is free to move only in the forward or backward direction, along the long axis of the corridor.

A single hypercube of a 4-D maze is shown in Figure 1D. Each barrier is not a square surface but a cube. Six distinct cubes are present, labeled in the figure as Cubes 1–6. Cube 1, the left-hand barrier, for example, has one hot surface (red colored) and one cold surface (blue colored), one upper surface, one lower surface, one near surface, and one far surface. The right-hand barrier, upper barrier, and lower barrier have a similar cubic structure. In addition, Cube 5, the red cube that appears to fill up the space inside the hypercube, serves as a barrier located at the hot side of the hypercube. The absence of this red cube would indicate that the hypercube is open in the hot direction and that the corridor extends in that direction. Cube 6, the blue cube that appears to fill up the space inside the hypercube, serves as a barrier at the cold side of the hypercube. The absence of this blue cube would indicate that the hypercube is open in the cold direction and that the corridor extends in that direction. Together, the six cubes shown in Figure 1D block movement toward the left, right, up, down, cold, and hot, and leave open movement forward or backward.

A subject's view of a 4-D maze is shown in Figure 1E. The corridor is viewed head on, extending in the forward direction and in the distance bending toward the right. The hypercube structure illustrated in Figure 1D is seen in Figure 1E as a repeating component of the corridor. Owing to normal linear perspective, the size of objects appears smaller in the distance. This decrease in apparent size with distance applies not only to the width and height of objects but also to their extent in the hot–cold dimension. Because a color cue is used to help indicate the hot–cold dimension, the distinction between blue and red becomes subtle for more distant objects.

The visual appearance of a 4-D corridor is considerably more complex if not viewed head on. Figure 1F shows a perspective on the same corridor as in 1E, after the subject has rotated partly in the R5 direction. It is this tremendously complex geometric mixing of dimensions, cubes, and surfaces that the subject must master to navigate through the 4-D environment.

Potential Caveats With 4-D Navigation

A small window on the 4-D world. The subjects were in actuality seated in a 3-D world in front of a 3-D computer. Did this immersion in an ambient 3-D world affect performance in a 4-D world viewed through a 15 × 15-cm window on the computer screen? Gamers are able to navigate through a virtual 3-D world displayed in a small window on a computer screen. The fact that the room around the gamer does not belong to the virtual world

does not appear to prevent the gamer from navigating through the mazes of the virtual world. We hoped that the same condition would apply to the 4-D world, that the subjects would learn to navigate the 4-D world, even though they saw it only through a window on the computer screen. It is possible that a more immersive 4-D environment, for example, using a larger screen or virtual reality goggles, might have enhanced learning. However, as detailed in the results, the data suggest that humans are able to learn to navigate the 4-D virtual environment under the present circumstances, and therefore a more immersive environment was not strictly necessary.

Memorizing example mazes. If only a small number of different maze configurations were possible, then subjects might be able to cheat, using trial and error on repeated exposure to determine the correct sequence of keystrokes for each maze configuration. However, this strategy was not feasible in the current experiment. The number of possible configurations for the 4-D mazes was 12,288 (6 possible directions for the first bend × 4 possible directions for the second bend × 2 possible directions for the third bend × 4 possible lengths for the first straight corridor segment × 4 possible lengths for the second straight corridor segment × 4 possible lengths for the third straight corridor segment × 4 possible lengths for the fourth straight corridor segment). Of these many possible maze configurations, 100 were randomly selected for the program library. When the subjects practiced 4-D mazes, the program randomly selected example mazes from this library of 100. Thus, subjects rarely encountered the same maze twice. Because subjects learned 4-D path integration in as few as 30 trials, they did not have sufficient opportunity to use trial and error over many exposures on each of the possible mazes.

Inextricable mixing of all four dimensions. Correct performance could not be achieved by treating the 4-D mazes as a normal 3-D world with an added stimulus quality that could be tracked separately. The reason is that the dimensions were not separable. They were entangled in the following manner. The subjects could translate only in the forward or backward direction. The subjects, therefore, were forced to turn around corners in a rotational manner. If a corridor turned to the left, for example, to follow the corridor the subject had to rotate leftward first, and then translate forward. As a result of these rotations, all four dimensions become spatially mixed. If the subject turned left, what was in front of the subject was reoriented to his or her right. What was behind the subject was reoriented to his or her left. If the subject turned upward, what was in front of the subject was reoriented below him or her. If the subject turned to the hot direction, was what behind the subject was reoriented to the cold of him or her. Corridors that extended in one direction with respect to the subject could, on rotation, come to extend in any other direction. All dimensions could be rotationally swapped with all others. For the subject to perform the task, his or her understanding of the spatial layout of the maze and memory of previously traversed corridor lengths had to be appropriately rotated with each new bend in the corridor, thus constantly mixing all four dimensions.

In a real-world office building, we use 2-D reasoning to navigate within each floor, and we add on a separate quality of height to navigate in elevation. However, this separation is possible only because we maintain our vertical orientation. Moving from floor to floor involves a vertical translation, not a rotation, and therefore there is no mixing of the height dimension with the horizontal

dimensions. However, consider a world without gravity in which moving upward requires rotating ourselves until what was once the wall is now the floor, and then traveling along that new floor. In such a world, height can no longer be treated as a separate quality from the horizontal directions. All three dimensions are interchangeable through rotation, and therefore navigation is impossible without a working knowledge of their rotational interactions. The 4-D mazes (and the 2-D and 3-D mazes) in the present experiment had this property that all dimensions could interact rotationally.

Stimulus qualities versus spatial dimensions. In the real world, the smell, sound, weight, or texture of an object are all “dimensions” in a colloquial sense but not in a geometric sense. For example, a heavy object remains heavy whether one examines it from one spatial perspective or another. The spatial dimensions, in contrast, have formal geometric interactions with each other that are not present for other attributes of objects. It is not difficult for humans to learn new stimulus qualities and to use those qualities to aid in navigation. However, to learn four interrelated geometric dimensions is fundamentally different from learning a stimulus quality because of the geometric rules of rotations and distances that are involved.

4-D reasoning versus 3-D pointing. In the 2-D mazes, the subjects pointed in the azimuth, utilizing one angular degree of freedom. In the 3-D mazes, the subjects pointed in azimuth and elevation, utilizing two angular degrees of freedom. Similarly, in the 4-D mazes, the subjects pointed using three angular degrees of freedom. Can it be said, therefore, that the 2-D mazes required 1-D reasoning, the 3-D mazes required 2-D reasoning, and the 4-D mazes required 3-D reasoning? If so, then successful performance on the 4-D mazes is not an indication of 4-D geometric ability. This explanation, however, is not compatible with the requirements of the task. To point accurately in the 2-D mazes, a subject must be able to mentally integrate corridor lengths in both dimensions. Consider a simple L maze in which a person walks 10 steps one direction, turns 90°, and walks 20 steps in the new direction. To point accurately back to the origin, the person must integrate the two lengths taking into account their orthogonality. Though the response may be expressed in terms of a single angle, the mental process behind the result requires a geometric integration of two dimensions. In an equivalent manner, the path integration task in the 3-D and 4-D mazes requires geometric integration of three dimensions and of four dimensions, respectively.

3-D reasoning to partially solve the 4-D task. It is possible for subjects to achieve better than chance performance in the 4-D mazes by relying entirely on 3-D geometric ability. With this strategy, the subject would be unable to integrate all four corridor segments but would in principle be able to integrate three corridor segments and thus partially solve the path integration task. Such a strategy could never lead to perfect pointing but could lead to better than chance pointing. It is therefore necessary to know the level of performance that can be achieved with this strategy.

To address this issue we used a simulated player. The simulated player had 3-D path integration ability and no 4-D path integration ability. It followed an ideal strategy for using its 3-D ability to partially solve the 4-D task. Each 4-D maze contained four corridor segments, each one aligned with a different dimension. The simulated player pointed back from the end point of the maze to the beginning of the second corridor segment. In this fashion, of

the four corridor segments, the simulated player took into account three of the segments, spanning three spatial dimensions. It performed path integration on three dimensions and did not incorporate a fourth dimension.

In reality, subjects did not have perfect 3-D path integration ability. For example, as detailed in the Results section, Subject 1 performed the 3-D mazes with an average angular error of 17°. One variant of the simulated player, SIM1, was also inaccurate in 3-D path integration, with a mean angular error of 17°. SIM1 pointed from the end of each 4-D maze to the beginning of the second corridor segment; the pointing was not accurate but was spread in a symmetric Gaussian distribution of angles around the desired angle, the width of the distribution adjusted such that the mean angular error was 17°. This strategy of sloppy pointing in three dimensions while ignoring the fourth dimension allowed SIM1 to achieve a mean accuracy for the 4-D task of 38°. In contrast, a strategy of random pointing achieves a mean accuracy of 90°.

A second variant of the simulated player, SIM2, was perfect in 3-D path integration. SIM2 pointed from the end of each 4-D maze to the beginning of the second corridor segment; the pointing was accurate, with an angular error of 0°. This accurate pointing in three dimensions while ignoring the fourth dimension allowed the simulated player to achieve a mean accuracy in the 4-D task of 28°.

SIM1 and SIM2 do not necessarily represent any strategy used by the human subjects. Rather, SIM1 and SIM2 provide benchmarks for the optimal performance possible in the 4-D maze given only 3-D ability. Any performance beyond those limits suggests the use of 4-D path integration.

Results

This experiment was designed around an individual-subject analysis. Enough data points were collected from each subject to determine whether the subject demonstrated path integration. We therefore first describe the pattern of results for one subject and then describe the results for the remaining subjects. Figure 2A shows the results for the 2-D mazes for Subject 1. Table 1 provides details of the statistical tests. Initially the mean pointing error (mean of first 10 runs) was $23.0^\circ \pm 21.7^\circ$, already significantly better than the chance level of 90°, $t(9) = 9.75$, $p = 4.4 \times 10^{-6}$. With practice this error declined (the linear downward trend was significant as tested with a standard linear regression model; $F(1, 128) = 10.70$, $p = .0014$) until, in the final 10 runs, the subject was able to point to the origin with a mean error of $7.9^\circ \pm 9.8^\circ$.

Figure 2B shows results for the 3-D mazes for Subject 1. Table 2 provides details of the statistical tests. Initially the mean error (mean of first 10 runs) was $38.1^\circ \pm 23.9^\circ$, significantly below the chance level of 90°, $t(9) = 6.86$, $p = 7.4 \times 10^{-5}$. With practice the subject improved (the linear downward trend was significant as tested with a standard linear regression model; $F(1, 260) = 15.63$, $p = 9.9 \times 10^{-5}$). After 262 runs the mean error (mean of final 10 runs) was $17.0^\circ \pm 13.6^\circ$.

Figure 2C shows the pointing data for the 4-D mazes. Table 3 provides details of the statistical tests. Initially the subject's mean angular error (mean of first 10 runs) was $97.2^\circ \pm 30.0^\circ$, not significantly different from the chance level of 90°, $t(9) = 0.76$, $p = .47$. As the subject practiced, the angular error dropped. This drop in error was rapid during approximately the first 20 runs (the

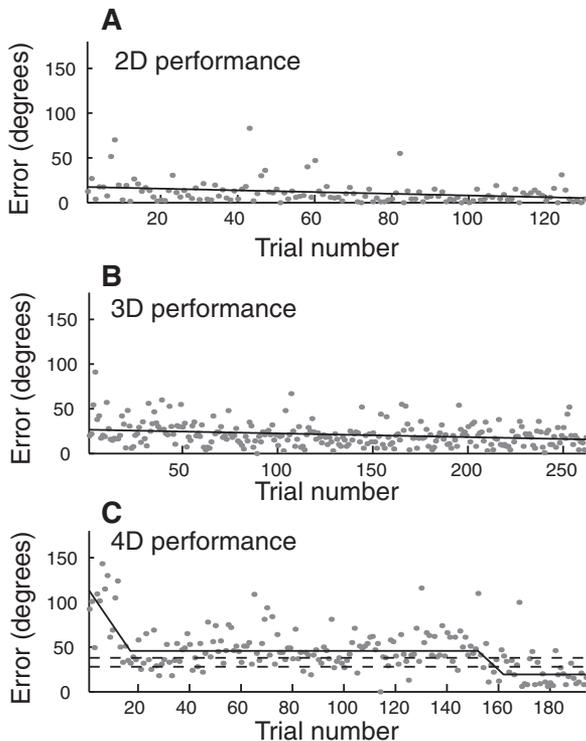


Figure 2. Results from Subject 1. A: 2-D performance. Pointing error as a function of run number. Chance performance is 90° . The subject began with better performance than chance and improved gradually. B: 3-D performance. Again the subject began with better performance than chance and improved gradually. C: 4-D performance. The performance began near chance and by Trial 20 improved to a level consistent with some 3-D ability in the 4-D world. After approximately 140 trials performance began to improve again, reaching a level consistent with true 4-D path integration. The fit lines show a model of two linear transitions and two steady states that was fit to the data by means of regression. The dotted lines show the performance achieved by two simulated players, SIM1 and SIM2. SIM1 (upper dotted line) was competent in 3-D to an error of 17° and had no 4-D ability. SIM2 (lower dotted line) was perfectly competent in 3-D (to an error of 0°) and had no 4-D ability. To show convincing evidence of 4-D ability, a subject had to perform significantly better than the SIM2 level.

linear downward trend during runs 1–20 was significant as tested with a standard linear regression model; $F(1, 18) = 11.96, p = .003$). The subject then stabilized during runs 20–140 at a mean angular error of $46.3^\circ \pm 17.3^\circ$ (the linear trend was not significant during runs 20–140 as tested with a standard linear regression model; $F(1, 119) = 0.48, p = .49$).

The level of performance during runs 20–140 was significantly better than the chance level of 90° , $t(120) = 27.75, p < 1.0 \times 10^{-10}$. Did this relatively good performance reflect competence in 4-D, or did it reflect the subject's ability to point in three of the four dimensions and thus at least partially solve the task? A computer simulation was run in which the simulated player was accurate in the three normal spatial dimensions and had no competency in the fourth dimension (see Method for more details of simulation). In SIM1, the simulated player was accurate in 3-D within a mean error of 17° , approximating the ability of the actual subject in 3-D. On the 4-D maze, SIM1 could point to the origin

of three of the four corridor links and thereby achieve a mean error rate of 38° , shown by the upper dashed line in Figure 2C. This dashed line therefore shows the best level of performance expected of Subject 1, if the subject were using 3-D ability to solve the 4-D task. The subject's actual mean error of 46.3° during runs 20–140 was not significantly better than this SIM1 level. Indeed the performance was significantly worse, $t(120) = 5.29, p = 5.62 \times 10^{-7}$. The subject's better than chance performance in the 4-D maze during runs 20–140 therefore cannot be convincingly attributed to 4-D competence. The performance could in principle have resulted from some use of 3-D spatial reasoning to partially solve the task.

A second simulated player (SIM2) was perfectly accurate in 3-D (0° angular error) and had no competency in the fourth dimension. SIM2 achieved an error of 28° in the 4-D maze (lower dashed line in Figure 2C). This error is the theoretical lowest mean error a player can achieve in the 4-D maze with perfect 3-D path integration ability. To demonstrate convincingly that the subject had gained real 4-D competence, the error rate would need to fall significantly below this stringent SIM2 level of 28° .

After approximately 140 runs, the subject's error began to fall again (the linear downward trend during runs 140–170 was significant as tested with a standard linear regression model; $F(1, 29) = 15.08, p = 5.4 \times 10^{-4}$). By the end of 194 runs the mean angular error (mean of final 10 runs) was $15.7^\circ \pm 7.5^\circ$, significantly below the benchmarks of SIM1 and SIM2: t test for SIM1, $t(9) = 9.46, p = 5.67 \times 10^{-6}$; t test for SIM2, $t(9) = 5.22, p = 5.5 \times 10^{-4}$. By this time the subject showed convincing evidence of spatial cognition in four dimensions.

In summary, the pattern of 4-D results for this subject is consistent with two phase transitions. Within the first 20 trials, the performance transitioned from chance level to a level that could in principle be explained by 3-D competence in a 4-D world and therefore is not adequate evidence of 4-D reasoning. It then remained at plateau until approximately Trial 140, when a second transition occurred to a level that could be explained only by 4-D competence. Because of this apparent series of transitions and plateaus, the data were fitted to a regression model that contained a linkage of four phases: a first downward linear phase, a first plateau phase, a second downward linear phase, and a second plateau phase. The free parameters determined by the regression included the initial y offset, the slopes of the downward linear phases, and the lengths of the first three phases. The regression analysis resulted in the fit line shown in Figure 2C, settling on transitions that occurred at runs 16, 152, and 162. The regression fit was statistically significant: standard regression model, $F(1, 188) = 24.83, p = 8.8 \times 10^{-16}$.

Figure 3 shows the 4-D results and regression fits for 5 subjects. Because subjects reached 4-D competence at different times, different numbers of runs are shown for each subject. The statistical results for all subjects are also given in Tables 1–3. Figure 3A replots the data from Subject 1 described above. Figure 3B shows that Subject 2 passed through similar phase transitions but at different times than Subject 1. Subject 2 began at chance level, within the first 25 trials dropped to a level that could in principle be explained by some 3-D competence within a 4-D world, remained at a plateau until Trial 60, and then dropped again to a level indicative of true 4-D competence. Subject 3 (Figure 3C) showed an even faster acquisition and a starker second transition. After the

Table 1
Statistical Results for All 5 Subjects on 2-D Mazes

2-D maze performance	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5
Number of trials	130	61	116	100	44
Total time (min)	70	31	49	125	25
Mean of first 10 trials	23.0 ± 21.7	8.9 ± 6.8	17.4 ± 12.5	20.5 ± 18.0	29.4 ± 27.9
Mean of last 10 trials	7.9 ± 9.8	3.7 ± 4.1	3.7 ± 3.5	1.9 ± 1.9	10.0 ± 16.2
Linear regression					
SS1, SS2	1677, 20068	217, 2503	1320, 8755	505, 13457	1130, 14585
<i>df</i> 1, <i>df</i> 2	1, 128	1, 59	1, 114	1, 98	1, 42
<i>F</i>	10.70	5.11	17.19	3.68	3.26
<i>p</i>	.0014	.02	6.5 × 10 ⁻³	.06	.08

Note. SS1 = sums of squares 1; SS2 = sums of squares 2.

first 16 trials the performance stabilized at a level consistent with some 3-D competence within a 4-D world, and at Trial 30 abruptly improved to a level indicative of true 4-D competence. Subject 4 (Figure 3D) showed an approximately similar pattern though with greater performance variability. The pattern for Subject 5 (Figure 3E) was different. Within approximately the first 75 trials this subject improved from chance to a level consistent with some 3-D competence within the 4-D world. The performance level remained at plateau until the end of the subject's participation, at Trial 161, with no evidence of 4-D competence. Because the subject stopped at Trial 161, it was not possible to determine whether, with more trials, the subject might have shown a similar pattern to the others, eventually transitioning to a level indicative of 4-D ability.

Discussion

The classical example of spatial adaptation through practice is prism adaptation (Held & Hein, 1958; Helmholtz, 1925). Prism adaptation involves a realignment of existing spatial maps that have been brought out of alignment by means of the prism. Learning to navigate within 4-D, however, cannot be accomplished by realignment of existing spatial constructs. The 4-D world is not a misalignment of familiar spatial properties. Instead it is topologically different from the familiar 3-D world. The present results suggest that the human brain is capable of learning 4-D path integration. This path integration implies an ability to

sum across changes in direction and lengths of path segments. It also implies an ability to perform spatial rotations correctly, in order to keep track of how corridor lengths extending in one dimension might, on rotation, come to extend in a different dimension. It implies a working knowledge of the manner in which each dimension can mix with the others.

Humans are adept at spatial updating, whether mentally rotating an object that has just been viewed, imagining themselves in a different perspective with respect to an array of objects, or updating a mental model of the environment while navigating through that environment (e.g., Boer, 1991; Diwadkar & McNamara, 1997; Easton & Sholl, 1995; Farrell & Thomson, 1998; Hintzman, O'Dell, & Arndt, 1981; May & Klatzky, 2000; Presson & Montello, 1994; Riecke, Cunningham, & Bultoff, 2007; Shepard & Metzler, 1971; Wraga, Creem, & Proffitt, 2000; Wraga et al., 2004). These abilities suggest that humans have a well-developed spatial machinery for keeping track of distances and locations despite movements and rotations. One possible interpretation of the present results is that this machinery is not rigidly built to compute within three dimensions. It is not, so to speak, a neuronal simulation of 3-D graph paper on which routes, angles, and distances can be plotted. Although we evolved in a 3-D world, our underlying spatial machinery is not built rigidly to handle the exact topology of the real world. Instead, the present results suggest that the machinery for spatial processing in the human brain is more flexible, handling general operations that are useful in spatial

Table 2
Statistical Results for All 5 Subjects on 3-D

3-D maze performance	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5
Number of trials	262	94	95	41	140
Total time (min)	214	162	81	114	107
Mean of first 10 trials	38.1 ± 23.9	30.4 ± 18.4	11.9 ± 11.4	30.9 ± 28.6	46.9 ± 24.2
Mean of last 10 trials	17.0 ± 13.6	13.3 ± 4.7	11.6 ± 20.8	6.6 ± 8.1	14.8 ± 13.2
Linear regression					
SS1, SS2	2586, 43014	1278, 13696	16, 17407	3860, 23053	2090, 50810
<i>df</i> 1, <i>df</i> 2	1, 260	1, 92	1, 93	1, 39	1, 138
<i>F</i>	15.63	8.68	0.08	6.53	5.68
<i>p</i>	9.9 × 10 ⁻⁵	.004	.77	.01	.02

Note. SS1 = sums of squares 1; SS2 = sums of squares 2.

Table 3
Statistical Results for All 5 Subjects on 4-D Mazes

4-D maze performance	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5
Number of trials	194	82	52	62	164
Time spent (min)	323	189	98	242	215
Mean of first 10 trials	97.2 ± 30.0	78.6 ± 28.1	64.3 ± 28.2	62.1 ± 29.3	72.5 ± 34.8
Mean of last 10 trials	15.7 ± 7.5	15.6 ± 6.6	7.6 ± 3.9	16.8 ± 8.8	28.1 ± 17.6
<i>t</i> test between SIM2 and last 10 trials					
<i>t</i> (9)	5.22	5.62	16.33	4.4	0.02
<i>p</i>	5.5 × 10 ⁻⁴	3.3 × 10 ⁻⁴	5.4 × 10 ⁻⁸	0.001	0.99
Linear regression					
SS1, SS2	49413, 74826	33817, 27942	26351, 10752	29166, 39756	43966, 82958
<i>df</i> 1, <i>df</i> 2	5, 188	5, 76	5, 46	5, 56	2, 161
<i>F</i>	24.83	18.50	22.54	8.21	42.00
<i>p</i>	8.8 × 10 ⁻¹⁶	5.6 × 10 ⁻¹²	2.3 × 10 ⁻¹¹	7.16 × 10 ⁻⁶	1.3 × 10 ⁻¹⁵

Note. SIM2 = second variant of simulated player; SS1 = sums of squares 1; SS2 = sums of squares 2.

cognition and that, with practice, can be applied to other spatial frameworks and other topologies.

Spatial Reasoning or Response to Low-Level Cues?

Because previous anecdotes of 4-D spatial ability have suffered from subjective reporting and from a lack of rigor, it is important to ask whether the performance of subjects in the present experiment can be explained in a low-level manner, such as by learning simple rules for responding to stimulus configurations, or whether it can be explained only by means of true 4-D geometric integration. Certain low-level explanations can be ruled out.

First, the task could not have been solved by using 3-D path integration alone, because the subjects significantly exceeded the performance that can be achieved by ideal 3-D path integration. Second, performance could not have been achieved by using 3-D reasoning and then adding a simple rule or trick to accommodate the corridor length in the extra fourth dimension. The reason is that the fourth dimension was not geometrically separable from the other dimensions. There was no corridor length intrinsically fixed in the fourth dimension. Rather, as the subject rotated in order to navigate through the maze, any corridor length could be, at different times, to the right or left, above or below, in front or behind, or to the hot or cold of the subject. Task performance required the subject to take into account the spatial structure of the maze even as it rotated in four dimensions.

Third, the 4-D visual cues could not have been used like regular stimulus qualities, such as odor or texture, to aid in navigation. Such stimulus qualities are sometimes called “dimensions” in a colloquial sense, but they are not dimensions in a geometric sense. They do not rotate in a rule-based fashion with respect to spatial dimensions. Spatial dimensions have a certain formal geometric interaction with each other that is not present for other attributes of objects. The path integration in the present experiment required the subjects to learn the manner in which the four dimensions interrelated spatially.

Comparison Among Subjects

Subjects 1–4 showed a similar pattern of results in the 4-D mazes. As each subject practiced, the maze performance under-

went an initial drop in error from chance level to a level that, though better than chance, could still in principle be explained as 3-D reasoning in the 4-D environment. The subjects’ mental strategies are not known. However, because 3-D reasoning could in principle have resulted in this level of performance, one cannot validly conclude that the subjects used 4-D reasoning in this phase. Performance then underwent a second transition to a second plateau level. This second level of performance was significantly better than could be achieved by ideal 3-D reasoning and thus implied some level of 4-D reasoning. Though Subjects 1–4 all showed this pattern of an initial fast improvement, a first plateau, a second improvement, and a second plateau, the timing of these events was different for different subjects. Subject 3 passed through these phases more rapidly than did the other subjects, reaching the second plateau phase by Trial 30. Subject 1 passed through these phases the least rapidly, reaching the second plateau by Trial 162.

One interpretation of these performance phases is that the initial drop in error, in the first 10 to 20 trials, corresponds to an initial familiarization with the keystrokes needed for navigation; the first plateau phase corresponds to the use of previously acquired 3-D reasoning to partially solve the 4-D mazes; the second drop in error corresponds to a period of increasing insight into the 4-D geometric structure of the mazes; and the second plateau phase corresponds to the new performance level achieved with the new 4-D spatial ability. In this interpretation, among Subjects 1–4, the initial familiarization with the navigation keys occurred over approximately the same timescale, within 10 to 20 trials. Also in this interpretation, the subjects varied in the amount of practice needed to begin to gain insight into the 4-D geometry, as the second plateau phase varied in duration from subject to subject. The reason for this variance is not clear. It is possible that the subjects varied in their intrinsic geometric skills, in their focus of attention on the task, in their experience with navigating through video games, or in other ways that might have impacted the task. The data in the present experiment do not suggest any specific explanation for this interindividual variation.

Subject 5 underwent the initial transition from chance level to the first plateau level in 75 trials, rather than the 10 to 20 trials

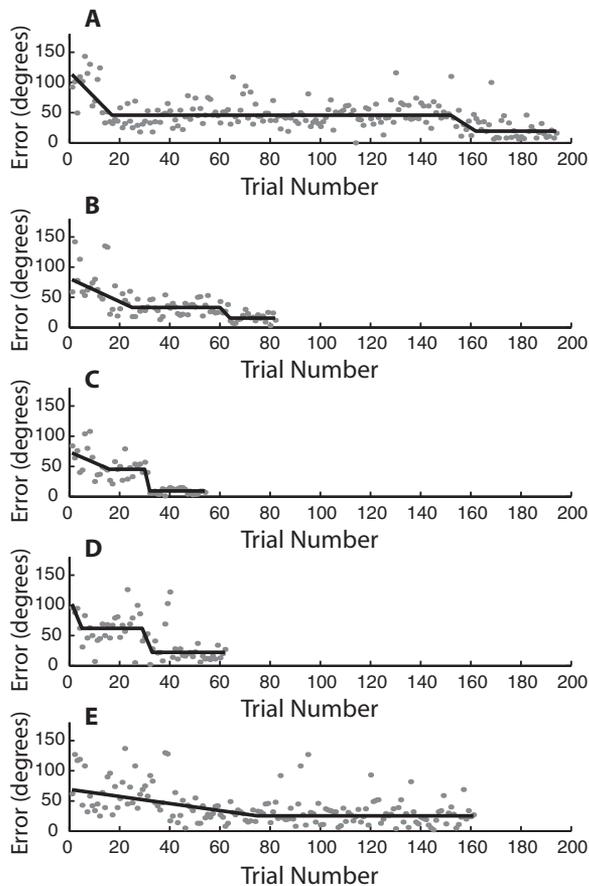


Figure 3. 4-D results for 5 subjects. A: Data from Subject 1 as in Figure 2C. B: Data from Subject 2 showing a similar two transitions in performance. C: Data from Subject 3 showing a particularly abrupt second transition. D: Data from Subject 4 showing an approximately similar pattern although with greater performance variability. E: Data from Subject 5 showing the first transition from chance level to a performance level consistent with some degree of 3-D reasoning in the 4-D world. This subject did not experience a second transition during the experiment.

required by the other subjects. Subject 5 then remained in the first plateau phase until quitting the experiment at Trial 161, without having entered a second transition or a second plateau phase. One interpretation is that this subject was in the process of experiencing the same performance phases as the other subjects, but on a longer time scale. A second interpretation is that this subject was intrinsically unable to perform 4-D path integration. The data do not distinguish between these two possibilities. It is of course possible that with more trials this subject would have eventually reached 4-D competence. The reason for the slower learning is once again not clear. The subject may have had weaker geometric skills, less focus of attention on the task, less experience with video games, or some other difference that impacted the task.

The present method used an individual-subject analysis. Enough data points were collected on each subject to determine with statistical reliability whether that subject could perform path integration in 2-D, 3-D, and 4-D. Interpreting the differences among

subjects, however, is difficult in the present design because of the small number of comparison points. The results suggest that there is some intersubject variance in this ability to learn 4-D path integration. Correlating that variance with other aspects of the subjects would require data from many more subjects before inferences could be drawn with statistical reliability. The present results suggest only that 4-D spatial reasoning can be learned by humans, whereas questions about the conditions that support different skill levels must wait for future research.

References

- Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology*, *199*, 219–224.
- Biegler, R. (2000). Possible use of path integration in animal navigation. *Animal Learning and Behavior*, *28*, 257–277.
- Boer, L. C. (1991). Mental rotation in perspective problems. *Acta Psychologica*, *76*, 1–9.
- Collett, T. S., & Collett, M. (2002). Memory use in insect visual navigation. *Nature Reviews Neuroscience*, *3*, 542–552.
- Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint independence in scene recognition. *Psychological Science*, *8*, 302–307.
- Easton, R. D., & Sholl, M. J. (1995). Object-array structure, frames of reference, and retrieval of spatial knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 483–500.
- Farrell, M. J., & Robertson, I. H. (2000). The automatic updating of egocentric spatial relationships and its impairment due to right posterior cortical lesions. *Neuropsychologia*, *38*, 585–595.
- Farrell, M. J., & Thomson, J. A. (1998). Automatic spatial updating during locomotion without vision. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *51(A)*, 637–654.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Gould, J. L. (1986, May 16). The locale map of honey bees: Do insects have cognitive maps? *Science*, *232*, 861–863.
- Held, R., & Hein, A. (1958). Adaptation to disarranged hand–eye coordination contingent upon reafferent stimulation. *Perceptual and Motor Skills*, *8*, 87–90.
- Helmholtz, H. V. (1925). *Treatise on physiological optics* (Vol. 3). Rochester, NY: Optical Society of America.
- Hintzman, D. L., O'Dell, C. S., & Arndt, D. R. (1981). Orientation in cognitive maps. *Cognitive Psychology*, *13*, 149–206.
- May, M., & Klatzky, R. L. (2000). Path integration while ignoring irrelevant movement. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*, 169–186.
- McIntosh, J. (2002). *The four dimensional maze game*. Retrieved April 2006 from <http://www.urticator.net/maze/>
- Menzel, R., Geiger, K., Joerges, J., Muller, U., & Chittka, L. (1998). Bees travel novel homeward routes by integrating separately acquired vector memories. *Animal Behavior*, *55*, 139–152.
- Muller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences, USA*, *85*, 5289–5290.
- Newcombe, N. S., & Huttenlochner, J. (2000). *Making space: The development of spatial representations and reasoning*. Cambridge, MA: MIT Press.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, England: Oxford University Press.
- Presson, C. C., & Montello, D. R. (1994). Updating after rotational and translational body movements: Coordinate structure of perspective space. *Perception*, *23*, 1447–1455.

- Riecke, B. E., Cunningham, D. W., & Bultoff, H. H. (2007). Spatial updating in virtual reality: The sufficiency of visual information. *Psychological Research, 71*, 298–313.
- Seyranian, G., Colantoni, P., & D’Zmura, M. (1999). Navigation in environments with four spatial dimensions. *Perception, 28* (Suppl. 7).
- Shepard, R. N., & Metzler, J. (1971, February 19). Mental rotation of three-dimensional objects. *Science, 171*, 701–703.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*, 189–208.
- Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: Coupling of egocentric and geocentric information. *Journal of Experimental Biology, 199*, 129–140.
- Wraga, M., Creem, S. H., & Proffitt, D. R. (2000). Updating displays after imagined object and viewer rotations. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*, 151–168.
- Wraga, M., Creem-Regehr, S. H., & Proffitt, D. R. (2004). Spatial updating of virtual displays during self- and display rotation. *Memory & Cognition, 32*, 399–415.

Received June 27, 2007

Revision received February 2, 2008

Accepted February 4, 2008 ■

**Call for Papers:
Special Section titled “Spatial reference frames: Integrating
Cognitive Behavioral and Cognitive Neuroscience Approaches”**

The *Journal of Experimental Psychology: Learning, Memory, and Cognition* invites manuscripts for a special section on spatial reference frames, to be compiled by Associate Editor Laura Carlson and guest editors James Hoffman and Nora Newcombe. The goal of the special section is to showcase high-quality research that brings together behavioral, neuropsychological, and neuroimaging approaches to understanding the cognitive and neural bases of spatial reference frames. We are seeking cognitive behavioral studies that integrate cognitive neuroscience findings in justifying hypotheses or interpreting results and cognitive neuroscience studies that emphasize how the evidence informs cognitive theories regarding the use of spatial reference frames throughout diverse areas of cognition (e.g., attention, language, perception and memory). In addition to empirical papers, focused review articles that highlight the significance of cognitive neuroscience approaches to cognitive theory of spatial reference frames are also appropriate.

The submission deadline is February 28, 2009.

The main text of each manuscript, exclusive of figures, tables, references, or appendixes, should not exceed 35 double-spaced pages (approximately 7,500 words). Initial inquiries regarding the special section may be sent to Laura Carlson (lcarlson@nd.edu). Papers should be submitted through the regular submission portal for JEP:LMC (<http://www.apa.org/journals/xlm/submission.html>) with a cover letter indicating that the paper is to be considered for the special section.