

# Spatial decisions and cognitive strategies of monkeys and humans based on abstract spatial stimuli in rotation test

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We showed previously that macaque monkeys (*Macaca mulatta*) could orient in real space using abstract visual stimuli presented on a computer screen. They made correct choices according to both spatial stimuli (designed as an abstract representation of a real space) and nonspatial stimuli (pictures lacking any inner configuration information). However, we suggested that there were differences in processing spatial and nonspatial stimuli. In the present experiment we show that monkeys could also use as a cue abstract spatial stimuli rotated with respect to the real response space. We studied the ability of monkeys to decode abstract spatial information provided in one spatial frame (computer screen) and to perform spatial choices in another spatial frame (touch panel separated from the screen). We analyzed how the monkeys were affected by the type of training, whether they perceived the stimuli as “spatial” or “nonspatial,” and which cues they used to decode them. We compared humans to monkeys in a similar test to find out which cognitive strategy they used and whether they perceive spatial stimuli in the same way. We demonstrated that there were two possible strategies to solve the task, simple “fitting” ignoring rotations and “remapping,” when the stimulus was represented as an “abstract space” per se.

spatial cognition | geometry of space | mental rotations

An ability to form and preserve a representation of space is crucial for most animal species including humans. The role of geometric information to construct such representations has been widely studied in recent decades.

In open space where the shape of the environment cannot be perceived as a cue, animals can orient using relative distances, directions and the position of multiple landmarks. Manipulation of these relationships could reveal whether animals can use features of the environment to deduce general geometric rules. One such test is an expansion test. Animals are trained with a goal hidden at a fixed location relative to an array of identical landmarks and after this training the distances between landmarks are changed, but the goal remains in a geometrically identical position (such as in the center).

This test has been carried out in many species: pigeons (1–3), marmoset monkeys, and humans. Only honey bees and adult humans spontaneously used a pure configuration strategy (4). In contrast to the experiments demonstrating an inability to infer an abstract geometric rule (1–5), Kamil and Jones (6) proved that Clark’s nutcrackers were able to learn geometric relations among two landmarks of varying distance. This finding was replicated in three avian species (7).

In other experiments, the ability to encode the global geometry of a closed enclosure was demonstrated in various species as reviewed by Cheng and Newcombe (8): in rats (9), in humans (10, 11), in monkeys (12), in birds (13), and in fish (14). Subjects trained to locate a goal in a corner of a rectangular enclosure were disoriented. After disorientation they searched in the correct position but also in the diagonally equivalent position. These decisions suggested that they were able to use geometric

properties of the enclosure for reorientation. This “rotational error” was taken as support for a “geometric module”—a central inner module encoding and manipulating only geometric information (9, 10, 15). However, recent research shows that featural nongeometric cues could inhibit or improve the learning of geometry itself (16–19).

Other experiments showed that animals could encode geometric features with no direct physical representation in the space, such as the center of enclosure. After animals learned to search at the center, the size or shape of the enclosure was changed. The results suggested that both birds and mammals were able to learn a geometric rule “search the center;” in certain circumstances, they searched at the distance corresponding to the training arena or used a mixture of information (20–24).

We developed behavioral tests to study the cognitive ability of monkeys to perceive visual stimuli presented on a screen and to perform spatial choices in real space based on these stimuli. We have demonstrated (25) that monkeys were able to use abstract visual stimuli on the screen to choose the correct position in real space (one of the touch holes in a certain position on a plastic board that served as a “response space”). We used “spatial stimuli” (designed as a representation of the response space and showing the configuration of touch holes) and “nonspatial stimuli” (pictures lacking spatial information). The monkeys were able to use both types of stimuli to orient in the real space, but differences in processing were observed. Further experiments showed that the monkeys could orient using spatial stimuli rotated against the response space they represented (26).

In the present experiments, we studied which strategy monkeys use to encode abstract spatial information from one spatial frame (computer screen) and to perform spatial choices in another spatial frame (touch panel separated from the screen). We analyzed whether they perceived the stimuli as “spatial” or “nonspatial,” which cues they used to decode them, and how they were affected by the type of training.

We also tested humans in a similar task to find out whether they use similar cognitive strategies to solve the task as monkeys.

## Results

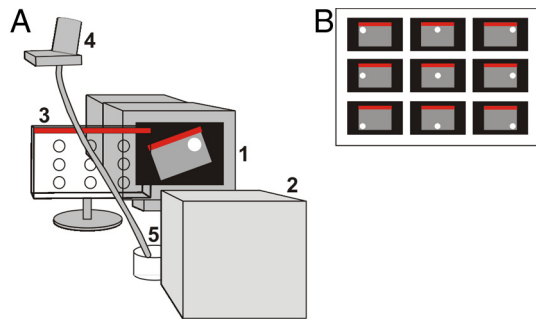
**Experiment A.** We trained the monkeys to choose one of the touch-holes in the response space (touch panel) according to the visual stimuli designed as a representation of this space and presented on the computer screen (Fig. 1A). The stimuli reflected the configuration of touch holes on the panel. They were rotated at different angles against the response space in the frontal plane.

The subjects should encode spatial information from the

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**Fig. 1.** Details of the apparatus used. (A) The scheme of the apparatus: 1, monitor; 2, box; 3, touch panel; 4, dosing device; 5, feeder. (B) The visual stimuli displayed on the screen: Relative positions of the circle in the rectangle represent the rewarded positions on the touch panel.

abstract stimuli and transform them into spatial choices in another spatial frame. Good performance would reflect their ability to use abstract stimuli as a cue to orient in real space. The type of errors they make could shed light on how they “map” the stimuli into the real space.

We used two types of training: Initially (phase 1), Attila (subject A) was trained with bigger rotation changes (with inserted zero rotation subphases), whereas Puck (subject B) was trained with stimuli rotated gradually in small rotation steps. In phase 2, the type of training was interchanged (see *Methods*).

The percentage efficiency (the ratio of the correct choices to the number of all choices) in Attila after each change of rotation (beginning from 40°) markedly decreased but rapidly returned to the previous high level (≈90%).

In phase 1 in Attila, the change of rotation from 0° led to a decrease from an average value of 91.8% counted from the last sessions of four zero-rotation subphases to 29.1% (60° rotation), 28.4% (80°), 20.8% (100°), and 21.7% (120°) in the first sessions after the change.

In phase 2, Attila was trained with gradually rotated stimuli, similarly as Puck was trained in phase 1. During phase 2, Attila did not show such a marked decrease of efficiency as in the comparable rotations in phase 1. After the change of rotation from −30° to −60° performance decreased from 87.7% to 41.5%. The change from −60° to −90° led to a decrease from 84.4% to 59.2% and the change from −90° to −120° to a decrease from 83.8% to 63.3%.

In contrast to Attila, Puck showed a smaller decrease after the gradual changes of rotation in initial subphases, but overall efficiency during training decreased. After the rotation to 120°,

performance decreased to 45.8% and in the next subphases did not increase to a level >50% even after a long training.

An analysis of the number of responses per correct choice (the number of incorrect choices before the correct position was selected) (Fig. 2) showed that the asymptotic performance of Attila averaged across all of the subphases was 1.18 ± 0.02 responses per correct choice. It decreased with stimulus rotation (Pearson’s correlation coefficient = 0.61, *P* < 0.001). However, the slope of the decrease was mild. The monkey needed 0.11 more choices per 90° of rotation away from zero to hit the target hole.

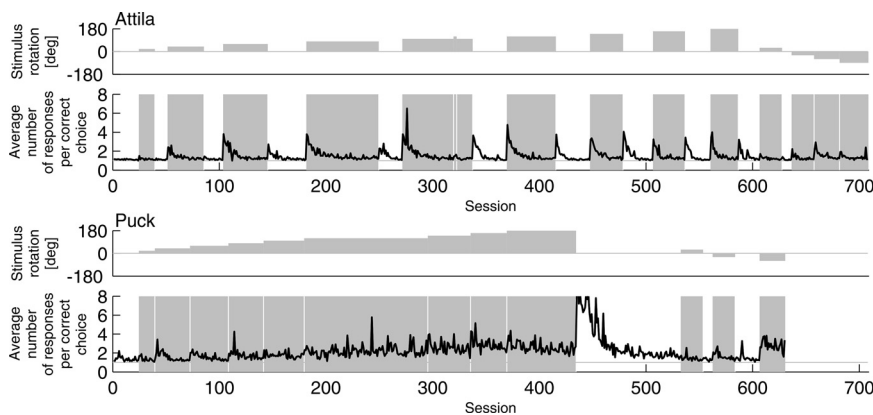
The performance of Attila immediately after rotation decreased markedly. The performance averaged across all of the first sessions after rotation (*n* = 25) was 2.71 ± 0.21 responses per correct choice. The performance depended on the magnitude of stimulus rotation (Fig. 2). For example, Attila needed 0.32 more choices to hit the target when the stimulus rotated from 100° to 120° (session 320), but needed 3.74 more choices when the stimulus rotated from 0° to 120° (session 370). The correlation between the magnitude of rotation and the change in the performance was significant (Pearson’s correlation coefficient = 0.76, *P* < 0.0001). The monkey needed 1.30 more choices per 90° of stimulus rotation to hit the target.

The asymptotic performance of Puck averaged across all of the 16 subphases was 1.72 ± 0.15 responses per correct choice. Similarly to Attila, the performance depended on the rotation (Pearson’s correlation coefficient = 0.68, *P* < 0.004). The monkey needed 0.59 more choices per 90° of rotation from zero to hit the target.

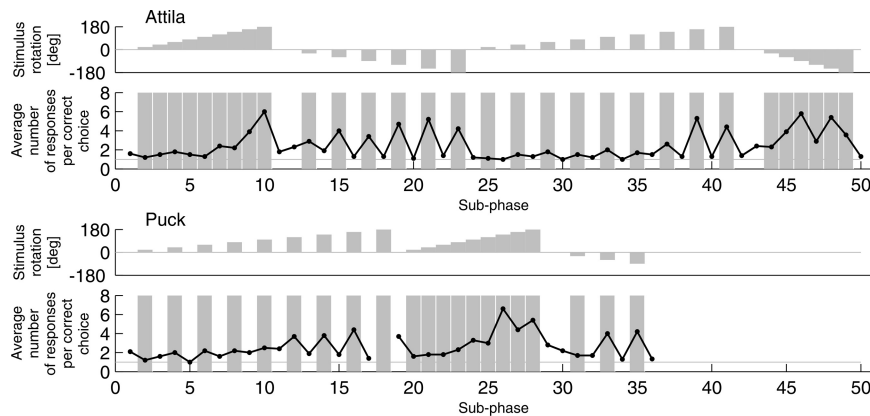
There are not enough data to confidently evaluate how the magnitude of rotation influences the performance in the first session after the rotation with respect to the preceding session. Fig. 2 indicates that a small change in rotation resulted in a small change in performance, whereas the two rotations >20° (180° in session 435 and −40° in session 607) resulted in a much bigger decrease of performance.

When the red stripe was removed from the stimulus at 90° rotation (in the control session at the end of Experiment A), Attila needed 3.50 responses per correct choice on average compared with 1.44 responses in the preceding session at 90° rotation with the red stripe. Puck needed 4.38 responses on average while needing 3.06 responses in the preceding session with the red stripe.

At asymptote, both monkeys responded to all of the nine stimuli with the same effectiveness (one-way ANOVA: Attila, *F*[8,223] = 0.98, *P* > 0.46; Puck, *F*[8,135] = 1.04, *P* > 0.31), but in the sessions immediately after rotation they did not respond



**Fig. 2.** Average no. of responses per correct choice per session during Experiment A (no. of choices until the correct position was selected). The upper line shows the rate of rotation.



**Fig. 3.** Experiment B: Average no. of responses per correct choice in monkeys (no. of choices until the correct position was selected). The upper line shows the rate of rotation.

to the stimuli equally well (one-way ANOVA: Attila,  $F[8,216] = 4.84$ ,  $P < 0.0001$ ; Puck,  $F[8,126] = 2.29$ ,  $P < 0.03$ ).

Attila responded better to the middle stimulus (no. 5) than to the left stimuli (no. 1, no. 4, and no. 7) and to the right stimuli (no. 3, no. 6, and no. 9) (Tukey-Kramer posthoc test:  $p$ 's  $< 0.05$ ). Stimulus no. 5 was in the center of the rotations and thus did not move after rotations. Attila needed  $1.27 \pm 0.25$  choices to respond correctly into hole no. 5 in the first sessions after the rotations whereas the best performance among the right and left holes was  $2.94 \pm 0.05$  choices per trial and to stimulus no. 2 and no. 8 was  $2.31 \pm 0.05$  and  $2.11 \pm 0.04$  choices per trial, respectively. Better responding to stimulus no. 5 could not be explained by a preferential response to hole no. 5. Attila responded to the hole no. 5 as frequently as to the holes on the left and to holes no. 2 and no. 8. Attila responded less frequently to the right holes (no. 3, no. 6, and no. 9) (one-way ANOVA:  $F[8,216] = 12.35$ ,  $P < 0.00001$ ; Tukey-Kramer post-hoc test:  $P < 0.05$ ).

Puck also responded differently to the stimuli in the first sessions after the rotations (one-way ANOVA:  $F[8,126] = 2.29$ ,  $P < 0.03$ ). However, the posthoc test showed no significant differences. Nevertheless Puck responded best to stimulus no. 2 ( $1.38 \pm 0.04$  responses per correct choice) followed by stimulus

no. 5 ( $1.65 \pm 0.05$ ) and stimulus no. 8 ( $1.97 \pm 0.11$ ). Puck also tended to respond less frequently to the right holes compared with the rest.

**Experiment B.** In Experiment B we tested how the monkeys and humans orient when the stimuli change their rotation during a single session.

Both humans and monkeys gradually increased the number of choices till the correct position was selected as a function of increasing rotation changes in both types of training (Figs. 3 and 4).

When the stimuli rotated within session, Attila performed best when the rotation was  $0^\circ$  ( $1.43 \pm 0.02$  responses per correct choice), followed by clockwise (CW) rotations ( $2.43 \pm 0.08$ ), and finally counter-clockwise (CCW) rotations ( $4.02 \pm 0.09$ ). All of these values were different (one-way ANOVA:  $F[2,47] = 25.58$ ,  $P < 0.00001$ ; Tukey-Kramer post-hoc test,  $P < 0.05$ ). Performance decreased with the magnitude of CW rotation, especially for large rotations (Fig. 3).

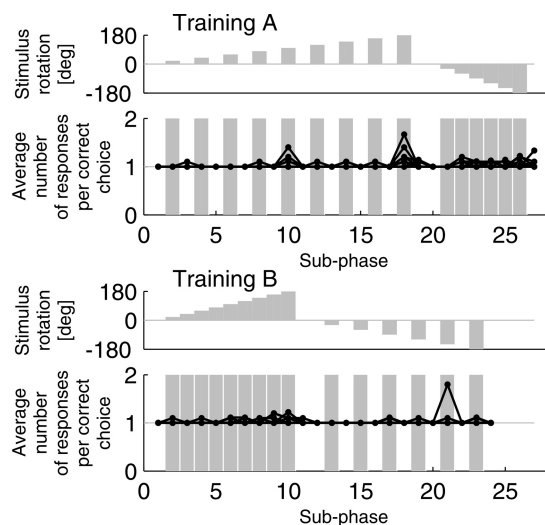
Puck's performance was also better when the stimuli were not rotated ( $1.92 \pm 0.05$  responses per correct choice) compared with its performance during CW rotations ( $3.07 \pm 0.09$ ).

Humans ( $n = 22$ ) performed very well in the task. They made few errors, especially when the stimuli were not rotated ( $1.004 \pm 0.002$  responses per correct choice). When the stimuli were rotated, they made slightly more errors ( $1.029 \pm 0.005$ ). The difference between the zero and nonzero rotations was significant (sign test: sign = 2,  $P < 0.001$ ). There was a tendency to make more errors during bigger rotations.

## Discussion

To determine one's position in an environment animals often use not only beacons directly marking a goal but also distances and directions between landmarks or selected features of the environment. Thus, they encode space as a geometric representation.

The question of whether the animals encode "global geometry" or "local geometric information" arose from studies where animals were trained to search a goal in a corner of rectangular or parallelogram arena. After reorientation they were tested in enclosures of transformed shapes (27, 28). Even if the transformation of shapes destroyed Euclidean parameters of the enclosure, after disorientation the subjects displayed nonrandom choices among the corners of the test arena. The authors concluded that the animals did not use global geometry for orientation but rather local geometric cues such as acute angles or ratio of walls length. In contrast, Cheng and Gallistel (29) argue that even if the animals did not use global shape, they



**Fig. 4.** Experiment B: Average no. of responses per correct choice in humans (no. of choices until the correct position was selected). The upper line shows the rate of rotation.



could use one of the global parameters for orientation—for example, the first principal axis.

We trained monkeys to choose a specific position in the response space (touch panel) according to abstract visual stimuli shown on the screen and separated from the response space. Thus, the subjects should encode spatial information from the abstract stimuli and transform them to the spatial choices in another spatial frame.

The results of Experiment A showed that rotation changes led to a decrease of performance and that these changes increased with increasing rotational changes. It agrees with findings in humans, where rotational tasks are often used (30). The pattern of responding differed among subjects: Subject A, with inserted zero-rotation subphases, performed with a sharp decrease of efficiency after rotation change and returned quickly to the previous level. In contrast, subject B, with gradual rotational changes, showed smaller decreases in efficiency after the change, but performed with a continual decrease of overall efficiency.

After the training was reversed, the efficiency of subject A did not decrease in comparable subphases as markedly as in the previous training of subject B. There was no overall decrease of efficiency, which could have been caused either by transmission of knowledge from previous training or by a different learning strategy of the monkeys.

It seems that gradual rotation changes made the task easier for monkeys than training with returns to the zero. The drop in efficiency after a return to zero-rotations could indicate that the monkeys in this training regime did not perceive the zero-rotations as “initial positions” but instead learned the stimuli again as new configurations.

The results clearly proved that animals could perform correct spatial choices in the real environment based on abstract stimuli. The monkeys made errors nonrandomly, indicating that they did not perceive the stimuli only as a set of separated patterns.

It seems that there were two possible strategies to perceive the stimuli and solve the task. The first was to fit positions directly as the presented positions were close to the positions in the real response space. This strategy was not affected by small rotations. The second strategy was to orient stimuli as a “relative space” per se, using cues that connect the positions on the screen with the positions in the real space (such as the red stripe).

When the stimuli were rotated only slightly, the monkeys indeed tended to fit positions directly. This behavior was demonstrated by the increasing number of errors in positions that became closer by rotations of stimuli to positions in nonrotated response space (position 1 became closer to position 2 with rotation 20° or 40°, position 3 become closer to positions 5 or 6, etc.).

In contrast, the monkeys were more efficient in responding to stimuli at the central position—the only position that did not change during rotation against the real space. This result suggests that they perceived this position as a cue and rotated the stimuli with relation to it. After rotation change in each subphase, they again remap the positions shown by the stimuli to the positions in the real space by using central position and other cues.

After the stimuli in Experiment A rotated from distinct angles to zero, efficiency decreased markedly. This result indicated that monkeys did not rely exclusively on the red stripe (distinct featural cue fitting stimuli to the real space) but that they used more distal cues including the monitor and other objects (“room frame”). However, the decrease of efficiency after removal of the red stripe indicated that it could be one of the used cues. Thus, the first strategy causes better performance with smaller rotation changes than the training with returns to zero positions.

This observation corresponds with findings in humans, who confirmed that they often used the simple “fitting strategy” in small rotations, and that they used relative space determined by the red stripe preferentially in big rotations. Contrary to mon-

keys in Experiment A the humans understood very well the representation of space by the red stripe on the screen reflecting the red stripe in the real space and thus they were almost without errors in the zero positions. This task was undeniably easier for humans, probably because of a common way to represent space by both experimenters and human experimental subjects.

However, in Experiment B the monkeys also performed markedly better in zero rotation subphases than in the analogous training in Experiment A. This observation could have been caused by the different type of training: In Experiment A they used reference memory, whereas in Experiment B they relied more on working memory, and this task was also more demanding of attention. This result could also have been explained by blocking in Experiment A: Once learned, a pattern of responses could block learning of another strategy. The phenomenon of blocking and overshadowing is now often discussed in spatial-orientation tasks (16, 17).

We proved that the monkeys could perceive the spatial features of abstract stimuli presented on the computer screen and use this information to orient in another spatial frame. Analogously to experiments mentioned above (27, 28) we could discuss whether the animals encode local cues or some global geometric parameters, but it seems that in this experimental design the monkeys used not only properties of the stimulus itself but also used objects in the room to orient the stimuli with regard to response space.

## Methods

**Subjects.** We used two male macaque monkeys (*Macaca mulatta*), 5 years old and housed in a collective cage. Water was freely available; standard food and fruits provided twice per day. Both monkeys were previously trained in the apparatus.

For Experiment B, we used 22 humans (11 males, 11 females) from 20–37 years. The human subjects provided informed consent.

All procedures were in accordance with Institutional and National Institutes of Health guidelines, with CR code and with the directive of the European Communities Council (86/609/EEC). The project was approved by the Ethical Committee of the 3rd Faculty of Medicine of the Charles University in Prague.

**Apparatus.** The apparatus consisted of an animal box, 21-inch monitor, a touch-panel, and a dosing device controlled by a computer. The monkeys were placed in front of the monitor in the box with an opened front wall allowing them to view the screen and to touch the panel embedded in the metal frame and placed alongside the monitor. The panel consisted of a transparent board with nine touch-holes in a 3 × 3 array (31 × 22 cm) and equipped by a photoelectric device registering the touch (Fig. 1A). Position 1 was in the top left and position 3 in the top right. A red stripe was on the upper edge of the touch-panel to fit stimuli and the response space.

**Stimuli.** The presented stimuli consisted of a rectangle and a bright filled circle shown in one of the nine possible positions in this rectangle. The rectangle represented the response space (panel) and the circle signaled the position of the rewarded touch-hole. The upper edge of the rectangle was marked by a red stripe reflecting the red stripe on the touch panel in the real space. The rectangle (18 × 13 cm) was displayed at the center of the screen. (Fig. 1B)

The orientation of the stimuli was initially the same as the orientation of the response space (touch panel). In the next phases, the stimuli were rotated on the screen, whereas the orientation of the response space was unchanged.

**Training. Experiment A.** The monkeys were trained to choose one of the touch-holes on the panel according to the visual stimuli presented on the computer screen. The stimulus was shown until the monkey responded. If the response was correct, the stimulus was switched off and the monkey was rewarded by sweet cereal pellets. After 3 s, a new stimulus was generated randomly. If the response was incorrect, the stimulus was switched off for 13 s and then the same stimulus was generated. The longer time interval after error served as a punishment.

The training consisted of three successive sessions (each from 50 stimulus presentations) per day. If the training exceeded 90 min, it was stopped.

The monkeys were trained in consecutive subphases differing in rotations. The two monkeys were trained differently. In phase 1, the stimulus for subject A (Attila) was rotated in CW direction for 20°, and after each rotation a zero

rotation subphase followed. The sequence was: 0°, 20°, 0°, 40°, 0°, 60°, 0°, 80°, 0°, 100°, 0°, 120°, 0°, 140°, 0°, 160°, 0°, 180°, and 0°.

For subject B (Puck), the stimuli were rotated gradually in CW direction for 20° without inserted zero-rotation subphases. The sequence was: 0°, 20°, 40°, 60°, 80°, 100°, 120°, 140°, 160°, 180°, and 0°.

In phase 2, the training was switched and different directions and angles of rotations were used to make the task unfamiliar. The sequence of rotations was: 0°, -30°, -60°, -90°, -120°, 0° (subject A) and 0°, -30°, 0°, -60°, 0°, -90°, and 0° (subject B).

**Experiment B.** In Experiment B, humans and monkeys were tested. The humans were divided into two groups differing in training. Each subject had two sequences of rotations (subphases) within one session:

Training A:

Sequence 1: 0°, 20°, 0°, 40°, 0°, 60°, 0°, 80°, 0°, 100°, 0°, 120°, 0°, 140°, 0°, 160°, 0°, 180°, and 0°.

Sequence 2: 0°, -30°, -60°, -90°, -120°, -150°, -180°, and 0°.

Training B:

Sequence 1: 0°, 20°, 40°, 60°, 80°, 100°, 120°, 140°, 160°, 180°, and 0°.

Sequence 2: 0°, -30°, 0°, -60°, 0°, -90°, 0°, -120°, 0°, -150°, 0°, -180°, and 0°.

- Spetch ML (1995) Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *J Exp Psychol Anim Behav Processes* 21:166–181.
- Spetch ML, Cheng K, MacDonald SE (1996) Learning the configuration of a landmark array: I. Touch-screen studies with pigeons and humans. *J Comp Psychol* 110:55–68.
- Spetch ML, et al. (1997) Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *J Comp Psychol* 111:14–24.
- MacDonald SE, Spetch ML, Kelly DM, Cheng K (2004) Strategies in landmark use by children, adults, and marmoset monkeys. *Learn and Motiv* 35:322–347.
- Collett TS, Cartwright BA, Smith BA (1986) Landmark learning and visuospatial Memories in gerbils. *J Comp Physiol A* 158:835–851.
- Kamil AC, Jones JE (1997) The seed-storing Corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature* 390:276–279.
- Jones JE, Antoniadis E, Shettleworth SJ, Kamil AC (2002) A comparative study of geometric rule learning by nutcrackers (*Nucifraga columbiana*), pigeons (*Columba livia*), and jackdaws (*Corvus monedula*). *J Comp Psychol* 116:350–356.
- Cheng K, Newcombe NS (2005) Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psych Bull Rev* 12:1–23.
- Cheng K (1986) A purely geometric module in the rat's spatial representation. *Cognition* 23:149–178.
- Hermer L, Spelke E (1994) A geometric process for spatial reorientation in young children. *Nature* 370:57–59.
- Learmonth AE, Nadel L, Newcombe NS (2002) Children's use of landmarks: Implications for modularity theory. *Psychol Sci* 13:337–341.
- Gouteux S, Thinus-Blanc C, Vauclair J (2001) Rhesus monkeys use geometric and nongeometric information during a reorientation task. *J Exp Psychol Gen* 130:505–519.
- Sovrano VA, Vallortigara G (2006) Dissecting the geometric module: A sense linkage for metric and landmark information in animals' spatial reorientation. *Psychol Sci* 17:616–621.
- Sovrano VA, Bisazza A, Vallortigara G (2002) Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition* 85:B51–59.
- Gallistel CR (1990) *The Organization of Learning* (The MIT Press, Cambridge, MA).
- Pearce JM, Ward-Robinson J, Good M, Fussell C (2001) Influence of a beacon on the spatial learning based on the shape of the test environment. *J Exp Psychol Anim Behav Processes* 27:329–344.
- Pearce JM, Graham M, Good MA, Jones PM, McGregor A (2006) Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *J Exp Psychol Anim Behav Processes* 32:201–214.
- Miller NY, Shettleworth SJ (2007) An associative model of geometry learning. *J Exp Psychol Anim Behav Processes* 33:191–212.
- Cheng K (2008) Whither geometry? Troubles of the geometric module. *Trends Cog Sci* 12: 355–361.
- Tommasi L, Gagliardo A, Andrew RJ, Vallortigara G (2003) Separate processing mechanisms for encoding of geometric and landmark information in the avian hippocampus. *Eur J Neurosci* 17:1695–1702.
- Tommasi L, Save E (2005) Generalization in place learning across geometrically different environments is impaired by hippocampal lesions in rats. *Neurobiol Learn and Mem* 84:1–8.
- Tommasi L, Thinus-Blanc C (2004) Generalization in place learning and geometry knowledge in rats. *Learn and Mem* 11:153–161.
- Tommasi L, Vallortigara G, Zanforlin M (1997) Young chickens learn to localize the centre of a spatial environment. *J Comp Physiol A* 180:567–572.
- Tommasi L, Vallortigara G (2000) Searching for the center: Spatial cognition in the domestic chick (*Gallus gallus*). *J Exp Psychol Anim Behav Processes* 26:477–486.
- Nekovarova T, Nedvidek J, Bures J (2006) Spatial choices of macaque monkeys based on abstract visual information. *Behav Brain Res* 174:93–100.
- Nedvidek J, Nekovarova T, Bures J (2008) Spatial choices of macaque monkeys based on the visual representation of the response space: Rotation of the stimuli. *Behav Brain Res* 193:204–208.
- Tommasi L, Polli C (2004) Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Anim Cogn* 7:53–59.
- Pearce JM, Good MA, Jones PM, McGregor A (2004) Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *J Exp Psychol Anim Behav Processes* 30:135–147.
- Cheng K, Gallistel CR (2005) Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi and Polli (2004). *J Exp Psychol Anim Behav Processes* 31:254–259.
- Shepard RN, Metzger J (1971) Mental rotation of three-dimensional objects. *Science* 171:701–703.

In each subphase, the stimulus was presented 10 times with rewarded positions generated pseudorandomly so that each position was presented at least once.

The humans, similarly to the monkeys, chose one of the touch-holes according to the visual stimuli on the screen, but with a 4-s time limit to respond. After an incorrect or no response, the same stimulus was generated. Presentations of a stimulus not followed by a response were not counted, thus in each subphase at least 10 choices occurred. Incorrect responses were followed by a sound signal.

The monkeys were trained without time-limit for response and with a reward for a correct choice. Both monkeys went through training A and B in 2 days. Puck went through training A first and then through training B, whereas Attila was trained in the opposite order.

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