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Rhesus monkeys manipulate mental images

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ABSTRACT

Humans form mental images and manipulate them in ways that mirror physical transformations of objects. Studies of nonhuman animals will inform our understanding of the evolution and distribution among species of mental imagery. Across three experiments, we found mostly converging evidence that rhesus monkeys formed and rotated mental images. In Experiment 1, monkeys discriminated rotations of sample images from mirror images, and showed longer response latencies with greater rotation as is characteristic of human mental rotation. In Experiment 2 monkeys used a rotation cue that indicated how far to mentally rotate sample images before tests, indicating a precision of better than 30° in discriminating rotations. Experiment 3 yielded mixed evidence on whether the rotation cue shortened decision times as has been found in humans. These results show that rhesus monkeys manipulate mental images.

Humans simulate the physical world with mental images, as when we visualize re-arranging furniture before physically moving it (Moulton & Kosslyn, 2009; Pearson & Kosslyn, 2015). Human mental images are characterized by at least three properties: 1) they partially recapitulate perception without concurrent perceptual input, 2) they are accessible to introspection, and 3) they can be manipulated in ways that parallel the physics of the objects mentally represented (Ganis, Thompson, & Kosslyn, 2004; Kosslyn, 1980, 1988; Neiworth & Rilling, 1987; Shepard & Cooper, 1982). Mental imagery may also be an important cognitive tool for other animals, particularly given the fact that other animals cannot use linguistic representation as do humans (Griffin, 1976; Premack, 1983).

Nonhumans have been reported to demonstrate two of the three characteristics of mental images described above. First, they clearly mentally represent some features of visual stimuli, partially recapitulating perception as is the case in humans. This is shown by the ability to accurately match to sample and do other kinds of visual cognitive tasks (e.g., Adachi, Kuwahata, & Fujita, 2007; Basile & Hampton, 2013; Bräuer & Belger, 2018; Miller, Erickson, & Desimone, 1996; Neiworth & Rilling, 1987). Second, two lines of evidence indicate that monkeys introspect about mental representations, a capacity sometimes known as phenomenal vision. Metacognition experiments show that monkeys know when they remember an image, indicating introspection (Basile, Schroeder, Brown, Templer, & Hampton, 2014; Hampton, 2001; Zakrzewski, Johnson, & Smith, 2017). "Blindsight" experiments show that monkeys, like humans, manifest at least two modes of visual perception, an implicit one and a potentially explicit mode (Andersen, Basile, & Hampton, 2014; Ben-Haim et al., 2021; Cowey & Stoerig, 1995; Moore, Rodman, & Gross, 2001). We address the third property of mental imagery here: that mental transformations parallel physical transformations.

Studies of human mental rotation were important in the "cognitive revolution," during which mental events gained credibility in scientific explanations of behavior. Researchers found that rotating a mental image shared properties with rotating a physical object. For example, it takes twice as long both to rotate a steering wheel 180° than 90°, and to visualize doing so. Participants in these studies decided whether a rotated shape was identical to, or a mirror image of, an upright comparison shape (Premack, 1983; Shepard & Metzler, 1971). The farther the shape was rotated, the longer it took to decide (Shepard & Cooper, 1982; Shepard & Metzler, 1971).

There have been comparatively few studies of mental rotation involving nonhuman animal subjects, and comparisons of the published work does not reveal clear relationships with ecological or phylogenetic variables. The first studies were done with pigeons, and these birds exhibited "rotational invariance." They were more accurate than expected by chance across rotations, but reaction time did not correlate with rotation (Hollard & Delius, 1982). Rotational invariance suggests

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that pigeons may not rely on manipulation of mental images to identify rotated objects. In a related but rather different test, pigeons were found to accurately anticipate the position of a temporarily occluded moving clock hand, but this is explained as readily by timing as by mental rotation (Neiworth & Rilling, 1987). Given that pigeons encounter objects in rapidly varying orientations while flying, they might have evolved processes that supports rapid recognition of objects in varying orientations without the time-consuming process of mental rotation (Hollard & Delius, 1982; Lohmann, Delius, Hollard, & Friesel, 1988). However, it could also be argued that other species, such as aquatic animals and arboreal primates could benefit similarly from rapid recognition of rotated objects and they have either been reported not to show rotational invariance, or show mixed patterns of behavior. A test of mental rotation in a single sea lion revealed evidence of mental rotation (Mauck & Dehnhardt, 1997). A study involving a single lion-tailed macaque, a largely arboreal species, reported the monkey erred more and was slower on rotation trials compared to non-rotation trials, but performance did not systematically change with angular rotation (Burmann, Dehnhardt, & Mauck, 2005).

Studies of mental rotation in terrestrial nonhuman primates report similarly inconsistent results. A study of Guinea baboons found evidence of mental rotation when stimuli were presented to the right visual field, however the findings did not replicate in another study by the same research group (Hopkins, Fagot, & Vauclair, 1993; Vauclair, Fagot, & Hopkins, 1993). Two studies involving rhesus monkeys reported either no evidence of mental rotation (Nekovarova, Nedvidek, Klement, Rokyta, & Bures, 2013), or mixed results of mental rotation where one of three monkeys showed the characteristic increase in response latency with angular rotation (Köhler, Hoffmann, Dehnhardt, & Mauck, 2005). In another study involving five rhesus monkeys, researchers reported a systematic decrease in accuracy as angular rotation increased, however reaction time was not reported (Parr & Heintz, 2008).

Some of the differences reported in the studies above may be due to differences in amount of training in the tasks used in these tests, or in prior experience subjects had manipulating objects in their lifetimes. Human children improve greatly in mental rotation tasks in the first five years of life (Frick, Hansen, & Newcombe, 2013), consistent with the possibility that experience and practice play a critical role (Newcombe, 2002). Here we provide a relatively large group of monkeys with extensive training to determine whether or not they are capable of mental rotation.

The variation in findings on mental rotation across species may be due to additional factors in addition to differences in training and experience. One interesting potential source of variation is cognitive differences that might associate with differences in behavioral ecology. For instance, the finding of rotational invariance in pigeons described above may reflect the need for pigeons to especially rapidly recognize rotated scenes and objects (Hollard & Delius, 1982). However, methodological differences between publications are also a likely cause of differences in findings. It is notable that few studies of nonhumans have used methods consistent with those detailed by Shepard and Metzler (1971) and subsequent human mental rotation studies. Requiring subjects to discriminate rotated images from mirror-images prevents subjects from using local features of stimuli to solve the task, and response latency is a critical outcome variable for assessing the correspondence between physical and mental rotation (Cohen & Kubovy, 1993; Delius & Hollard, 1995; Shepard & Cooper, 1982). Use of mirror-image stimuli and/or response latency have not always been reported in nonhuman studies (Nekovarova et al., 2013; Parr & Heintz, 2008). Comparing findings across species would be facilitated by a more standardized approach using these core features of the work done with humans. In this study, we developed a monkey analog of the mental rotation task using a delayed match-to-sample procedure with mirror image discrimination stimuli and both latency and accuracy as outcome measures.

In Experiment 1 monkeys demonstrated the hallmark of mental rotation, taking longer to find a matching shape the more the shape was rotated. In Experiment 2 monkeys used a cue that indicated how far to mentally rotate an image while the image was out of sight. In Experiment 3 we tested whether this rotation cue would speed identification of rotated images using the procedure from Experiment 1. Findings from Experiment 3 were mixed.

1. Experiment 1

Monkeys were trained in a mental rotation task that closely paralleled methods used with humans (Fig. 1A, Cooper & Shepard, 1973; Vauclair et al., 1993). Monkeys studied two-dimensional shapes that disappeared after they touched them. After 500 ms the studied shape and its mirror image appeared, both rotated up to 120°. Monkeys were rewarded for selecting the rotated version of the studied shape, avoiding the mirror image. Critically, mirror images contain identical geometric features, making it impossible to identify the rotated match by features alone (Cooper & Shepard, 1973; Shepard & Metzler, 1971). We hypothesized that if monkeys mentally rotate images, and such rotation takes time, as it would if done physically, then they would take longer to find the correct shape the more it was rotated (Shepard & Cooper, 1982).

1.1. Subjects

We tested six adult male rhesus monkeys (*mean age: 9.8 years old*) that had extensive experience with cognitive testing and match-to-sample tasks. Monkeys had ad libitum access to water and received their daily caloric intake through a combination of nutritionally balanced reinforcement pellets and monkey biscuits. They were individually housed due to social incompatibility but had visual and acoustic contact with conspecifics. Procedures complied with U.S. law, the National Research Council guide for the care and use of laboratory animals, and were approved by the Emory University Institutional Animal Care and Use Committee.

1.2. Apparatus

Computerized testing systems were mounted on monkeys' home cages and consisted of a touch-sensitive LCD monitor (Elo TouchSystems, Menlo Park, Ca), two food dispensers (Med Associates Inc., St. Albans, VT), and were controlled by custom programs written in Visual Studio 2013 (Microsoft Corporation).

1.3. Procedure

Monkeys performed a match-to-sample task with mirror image distractors (Fig. 1A). Trials were initiated by touching a green start square twice. A sample shape then appeared centrally on screen. Samples were drawn from a pool of 10 stimuli: 5 shapes and their mirror images (Fig. S1). After touching the sample shape twice, the screen went blank for 500 ms. At test, the sample shape and its mirror image were presented side by side, both rotated either 0°, 30°, 60°, 90°, or 120°. The position of the target and distractor were counterbalanced across trials. Selections of the rotated sample shape were followed by a reinforcing food pellet, positive audio feedback, and a 3-s inter-trial interval. Selections of the mirror image shape were followed by negative audio feedback and a 6-s time-out. All 10 stimuli appeared once as the correct response at each angle, randomly distributed in each 50-trial session. Testing concluded for each monkey when it had completed at least 20 sessions and accuracy was significantly above chance at all orientations simultaneously over the last two blocks of five sessions (significance at $p < .05$ as determined by binomial tests conducted for each orientation individually).

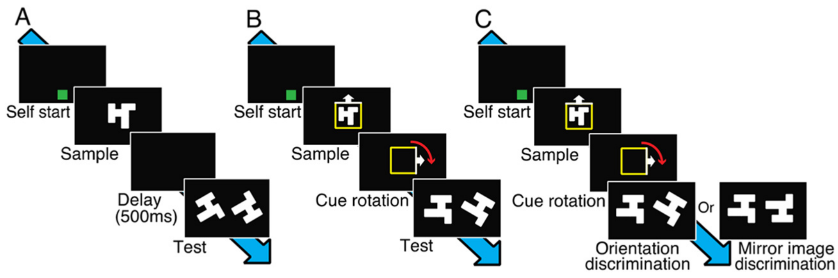

Fig. 1. Procedures used to test mental imagery in monkeys. (A) Mirror image discrimination (Experiment 1): Monkeys started trials by touching the green square twice. After touching the sample shape, the screen was blank for 500 ms, followed by a mirror image discrimination test. (B) Cued angle discrimination (Experiment 2): The sample shape was touched, it disappeared, and the cue rotated. Monkeys were rewarded for selecting the image that was rotated to the extent indicated by the cue. (C) Cued mirror image and orientation discrimination (Experiment 3 Cued Phase): Following cue rotation, monkeys made mirror image and orientation discriminations in pseudorandom order. In final testing, monkeys repeated Experiment 1 for comparison. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1.4. Results and discussion

Analyses of reaction time here and throughout used correct trials only. Across all conditions, monkeys averaged 79% correct, meaning that on average 21% of trials were not included in the analysis of reaction time because monkeys chose incorrectly on these trials. Monkeys took longer to respond on trials with greater rotation, matching the signature of mental rotation in humans (Fig. 2, upper panel; rmANOVA: $F_{(4,\ 20)} = 26.551$, $p < .001$, $\eta_p^2 = 0.841$; Shepard & Cooper, 1982; Shepard & Metzler, 1971). While this result is a clear parallel with human mental rotation, our monkeys differed from typical results from humans in that accuracy was lower for larger rotations (Fig. 2, lower panel; rmANOVA: $F_{(4,\ 20)} = 7.822, p = .001, \eta_p^2 = 0.605$). Longer response times and greater transformation may have caused forgetting or distortion of mental images, resulting in the decrease in accuracy found with greater rotation. A decrease in accuracy is not inconsistent with mental rotation, and we mitigated the possible effect of differences in accuracy on latency by only analyzing latencies from correct trials. Nonetheless, because longer latencies often accompany guessing (e.g., Hampton, 2009), the increase in latency could plausibly result from monkeys guessing more with larger rotations, rather than from the time-consuming process of mental rotation.

To address the potential confounding of response latency and accuracy in Experiment 1, we used accuracy instead of latency as the primary basis for inferring mental rotation in Experiment 2. This task does not directly test for mental rotation, in the sense of temporally extended incremental change of a mental representation by rotation around an axis. However, success in this task does require accurate transformation of a mental representation while preserving the fidelity of the correspondence between the mental representation and the represented image. In Experiment 2, monkeys discriminated identical shapes that differed only in orientation, ruling out discrimination on any basis other than orientation.

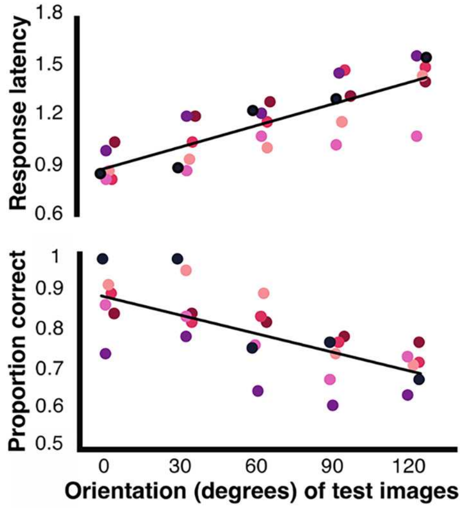

Fig. 2. Monkeys took longer to respond and were less accurate with more rotation. (Top) Median response latency(s) on correct trials; (Bottom) proportion correct.

2. Experiment 2

Monkeys were cued to mentally rotate a sample shape to a specific orientation. At test they saw two identical shapes; the target was rotated the cued amount, and the distractor was rotated 30° more or less than the target (Fig. 1B). The cue specified the amount the target would be rotated at test, but monkeys were not shown the target rotating. If monkeys rotate mental images, they should rotate them on cue to identify the target.

2.1. Subjects & apparatus

The same subjects, stimuli, and apparatus used in Experiment 1 were used in Experiment 2.

2.2. Procedure

Monkeys learned in stages that a cue indicated the extent to which a target image would be rotated from the sample orientation.

2.2.1. Initial rotation discrimination training

After monkeys initiated a trial, a sample shape appeared surrounded by a rotational cue (Fig. 1B). Monkeys touched the sample shape causing the shape and the cue to rotate clockwise 0°, 30°, 60°, 90°, or 120°. All rotations took the same amount of time, and involved the same number of animation frames, with each frame involving a larger movement for larger rotations. For example, on a 30° trial, the shape and cue were erased and drawn 30 times, rotating clockwise by 1° each time; on a 120° trial, they were also erased and drawn 30 times, but rotated clockwise by 4° each time. The duration of the rotation animation was approximately 950 milliseconds across all rotations, with a standard deviation of 65 milliseconds. The cue and sample remained onscreen for 500 ms after rotation was complete. The test appeared after the screen was blank for 500 ms. Both test choices were the previously seen shape. The target was rotated to the cued orientation, and the distractor was rotated +/− 60° relative to the target. The left-right position of the target on the screen, and whether the distractor was rotated more or less than the target, was counterbalanced across trials. Each target orientation was used with each shape twice per session in a randomized sequence, once with a distractor at −60° and once with a distractor at +60°, yielding sessions of 100 trials. After monkeys were significantly above chance simultaneously at each orientation (significance at $p < .05$ as determined by binomial tests conducted for each orientation every 5 sessions) the difference between the targets and distractors was reduced to 30°. After again meeting criterion, monkeys progressed to the next stage of training.

2.2.2. *Sample shape fading*

Monkeys learned to follow the rotational cue in the absence of the target image rotating inside it. We removed the sample shape before the cue had completed rotating. The point at which the target shape disappeared was pseudorandomly determined from among 10 possible points between 67% and 100% of the total rotation achieved by the cue. Monkeys again had to reach criterion. This process was repeated with the sample shape disappearing between 33% and 67% and finally between 0% and 33% of cue rotation.

2.2.3. *Cue only tests*

The sample shape disappeared immediately after being touched, and the cue then rotated to the to-be-tested orientation without the sample shape. Monkeys completed this phase when they met the same accuracy criterion used in training.

2.3. *Results and discussion*

Monkeys learned to discriminate the shapes at the cued orientation from distractors rotated $+/- 30^\circ$ ($p \leq .05$ by binomial tests at each orientation; see Table 1). Monkeys therefore mentally rotated the sample shape to the cued orientation with a fidelity better than 30°, even though the orientation of the target shape was indicated only by the cue and the shape itself did not visibly rotate. Monkeys were also significantly slower to respond when the amount of rotation dictated by the cue was large ($F(4, 16) = 4.518, p = .012$). These results indicate mental imagery by showing that monkeys formed detailed shape representations and mentally transformed them with fidelity to match stimuli presented on the computer screen. These results show that monkeys are capable of rotating mental images on cue, but because the monkeys required extensive training to attain this level of performance, we should be cautious inferring that monkeys would do this in nature, or even that such opportunities would arise naturally. These results are important because Experiment 1 and Experiment 2 used different approaches and dependent measures yet converged on the conclusion that monkeys rotate mental images.

One alternative interpretation of the findings from Experiment 2 is that monkeys used the orientation of the horizontal or vertical sides of the cue to guide their choice at test. The upright and horizontal faces of the rotational cue and the target shape align when oriented at the same angle (Fig. 1B). A monkey might solve this task by matching the vertical or horizontal faces of the cue at the time the cue disappeared, with the faces of the choice shapes at test. If monkeys used this strategy, accuracy should not vary as a function of the extent of cue rotation because the difficulty of matching the orientation of the cue at offset with the test images is the same regardless of rotational distance. By contrast, the more a mental image is transformed, the more likely it is to be forgotten or distorted, leading to more errors with larger rotations. Monkeys were significantly less accurate on trials with greater cue rotation, consistent with mental imagery and mental rotation (main effect of cued angle: $F_{(4, 16)} = 11.509$, $p < .001$; see Table 1 for individual data), but not the alignment hypothesis. We further evaluated the alignment hypothesis in Experiment 3. We required monkeys to discriminate images that did not differ in alignment with the rotational cue, but that again differed in the mirror image dimension, as in Experiment 1. Success in the task in Experiment 3 cannot be achieved using alignment.

Table 1
Accuracy across rotations for the last 6 sessions of Experiment 2. All 6 monkeys were significantly more accurate than expected by chance as determined by binomial tests.

		Orientation (Degrees) of test images				
		0°	30°	60°	90°	120°
Subject	A	0.96	0.79	0.73	0.82	0.68
	B	0.76	0.85	0.69	0.75	0.72
	G	0.92	0.79	0.81	0.76	0.64
	Sh	0.92	0.85	0.73	0.65	0.66
	Sy	0.86	0.82	0.65	0.70	0.82
	V	0.92	0.78	0.69	0.69	0.66

3. Experiment 3

When humans are cued about the orientation in which test shapes will appear, they rotate their mental images to the correct orientation before tests, eliminating the longer response times found with larger rotations (Cooper, 1976; Cooper & Shepard, 1973; Suchan, Botko, Gizewski, Forsting, & Daum, 2006). In Experiment 3, monkeys repeated the mirror image discrimination task from Experiment 1, but were either cued, or not cued, about the orientation in which the test stimuli would appear. We compared response times on cued mirror image tests (Fig. 1C) to those from a block of uncued trials from Experiment 1 and a block of uncued trials run at the end of Experiment 3 (Fig. 1A). If monkeys mentally rotated images when cued, then they, like humans, should show less increase in response times with rotation on cued trials compared to uncued trials. Critically, monkeys could not select the correct image in the mirror image discrimination tests by using the cue alone, as they did in Experiment 2 because the task was mirror image discrimination and both the target and the distractor appeared at the same orientation.

3.1. *Subjects & apparatus*

The six monkeys and the materials from Experiment 2 were used again.

3.2. *Procedure*

Monkeys first completed a block of trials using the procedure from Experiment 2, except two types of tests were pseudorandomly intermixed (Fig. 1C). Half of trials were mirror image discrimination trials, the other half of trials were orientation discrimination trials, yielding a total of 200 trials per session. Intermixing the two types of trials ensured that monkeys continued to use the rotational cue, because half of the time they needed it to discriminate on the basis of orientation, and the correct orientation could only be known from the cue. Monkeys were required to perform significantly above chance across all angles for 2 consecutive 5-session blocks (significance at $p < .05$ as determined by binomial tests conducted for each orientation every 5 sessions). This performance criterion was applied to orientation discrimination trials only, and performance on mirror image trials did not influence whether or not a monkey met criterion. Upon meeting this criterion, we planned for monkeys to proceed to the final block of mirror image discrimination trials without the rotational cue (but see results, below). We intended to use this final block of trials for a comparison of response latencies on cue and uncued trials. Collecting these comparison trials from the final phase of testing ensured that continued training could not account for any flattening of the latency function observed in the cued trials. Monkeys were intended to complete the uncued block of trials after meeting the same performance criterion used in Experiment 1.

We first compared performance on the last 10 sessions of cued mirror image trials with performance on the uncued mirror image trials collected during Experiment 1. We also compared these same cued mirror image trials with a final block of 10 sessions of uncued mirror image trials collected as the last part of Experiment 3.

During the initial administration of Experiment 3, a programming error caused the rotational cue to disappear on the majority of trials immediately after monkeys touched the sample. The coding error also affected randomizing of the left and right position of correct choices, allowing monkeys to complete the task without the aid of the cue. The programming error was only noticed after monkeys had completed Experiment 3. We therefore retrained monkeys to use the cue by having them complete the procedures described in Experiment 2, following which they were given the correct version of Experiment 3 described above.

Only 1 monkey reached criterion. Two monkeys who were near criterion were moved from the cued phase of Experiment 3 to the uncued phase before reaching criterion because the novel coronavirus was set to interrupt lab operations for an indefinite duration. Testing of the final three monkeys was paused and resumed later in the year, after laboratory operations resumed. After extensive training without fully reaching criterion (92, 98, and 104 days) the final three monkeys were moved from the cued to uncued phase of testing without having met criterion. All monkeys completed at least 200 sessions, and therefore, we analyzed their cued test data from sessions 191–200. All six monkeys reached criterion on the uncued phase of testing.

3.3. Results and discussion

This compound task, intermixing cued and uncued trials unpredictably was clearly difficult for the monkeys. We performed two analyses for Experiment 3. First, we compared cued mirror image performance to uncued mirror image performance collected prior to cue training in Experiment 1. A strength of this comparison is that it allows us to compare mental rotation performance prior to and after training that ostensibly caused them to mentally rotate prior to test images appearing. A weakness of this comparison is that comparatively better performance on cued trials might be expected simply because the monkeys had more experience with mental rotation by Experiment 3. Therefore, we performed a second analysis where we compared performance on cued mirror image trials and uncued mirror image trials collected after cue training and test, at the very end of Experiment 3, when monkeys had the maximum practice. The strength of this comparison is that monkeys experience with mental rotation was approximately equal at the time the cued and uncued data were collected. A weakness of this comparison is that monkeys have, at this point, been trained extensively to rotate images prior to the appearance of tests. If they continue to execute this rotation whether or not a rotation cue appears, the difference between cued and uncued trials might not be evident.

Compared to their performance on the uncued Experiment 1 test, the rotation X response time function was flatter in sessions with the rotational cue (Fig. 3 Left; rmANOVA, rotation X cue interaction: $F_{(1,\ 5)} = 28.930$, $p = .002$, $\eta_p^2 = 0.302$; cued vs uncued: $F_{(1,\ 5)} = 4.802$, $p = .079$, $\eta_p^2 = 0.386$; rotation: $F_{(1,\ 5)} = 49.748$, $p = .001$, $\eta_p^2 = 0.728$). Monkeys were also overall more accurate on cued trials relative to Experiment 1 (rmANOVA, cued vs uncued: $F_{(1,\ 5)} = 13.927$, $p = .013$, $\eta_p^2 = 0.569$; rotation: $F_{(1,\ 5)} = 39.174$, $p = .001$, $\eta_p^2 = 0.725$; cue X rotation interaction: $F_{(1,\ 5)} = 0.115$, $p = .748$, $\eta_p^2 = 0.004$). Although this comparison provides evidence that is consistent with cued mental rotation studies in humans, it is important to recognize that the Experiment 1 data were collected at a time when monkeys were comparatively less experienced at mental rotation tasks. Thus, it is unclear to what extent the observed significant differences in latency and accuracy are due to the rotational cue or simply experience. One reason to believe it is not solely because of experience is that the cue caused a comparatively greater reduction in latency with larger rotations compared to smaller rotations. If monkeys were simply getting better without using the rotation cue, then we would expect latencies to improve uniformly across degrees of rotation. Comparing uncued latency functions between Experiment 1 and Experiment 3 shows that the slope flattened significantly (rmANOVA, Experiment 1 vs Experiment 3: $F(1, 5) = 1.79$, $p = .239$, $\eta p^2 = 0.213$; rotation: $F(1, 5) = 55.80$, $p < .001$, $\eta p^2 = 0.587$; test X rotation Interaction: $F(1, 5) = 11.90$, $p = .018$, $\eta p^2 = 0.218$).

In contrast to the results reported above, and in contrast to results from humans, performance on uncued trials following cue training did not differ from that on cued trials, although the effect of rotation was still present (Fig. 3 Right; rmANOVA, rotation X cue interaction: $F_{(1,\ 5)} = 0.105$, $p = .758$, $\eta_p^2 = 0.002$; cued vs uncued: $F_{(1,\ 5)} = 0.089$, $p = .776$, $\eta_p^2 = 0.012$; rotation: $F_{(1,\ 5)} = 37.240$, $p = .001$, $\eta_p^2 = 0.529$; Cooper, 1976; Cooper & Shepard, 1973; Suchan et al., 2006). Moreover, the rotational cue did not significantly increase accuracy (rmANVOA: cued vs uncued: $F_{(1,\ 5)} = 0.757$, $p = .424$, $\eta_p^2 = 0.033$; rotation: $F_{(1,\ 5)} = 21.431$, $p = .005$, $\eta_p^2 = 0.699$; rotation X cue interaction: $F_{(1,\ 5)} = 2.138$, $p = .203$, $\eta_p^2 = 0.087$). Thus, the first comparison supports the hypothesis that the rotational cue causes monkeys to rotate images before test, flattening the rotation X response latency function, but the second comparison does not.

One explanation for why performance did not differ between cued and uncued trials in the second comparison is that monkeys continued to mentally rotate images prior to test on both cued and uncued trials, due to their extensive training with cued trials just prior to these final tests. The focus of Experiment 3 was on whether monkeys would use the rotational cue to mentally rotate in advance of tests. While the evidence that monkeys could mentally rotate fully in advance of tests is mixed, we consistently observed longer latencies with larger rotations, replicated again here. Regardless of whether latency and accuracy functions flattened because of the rotational cue or because of experience, monkeys still showed a relation between extent of rotation and accuracy and latency, and this pattern is characteristic of mental rotation. Throughout these three experiments, we consistently observed this pattern.

4. General discussion

We found multiple independent signatures of mental imagery,

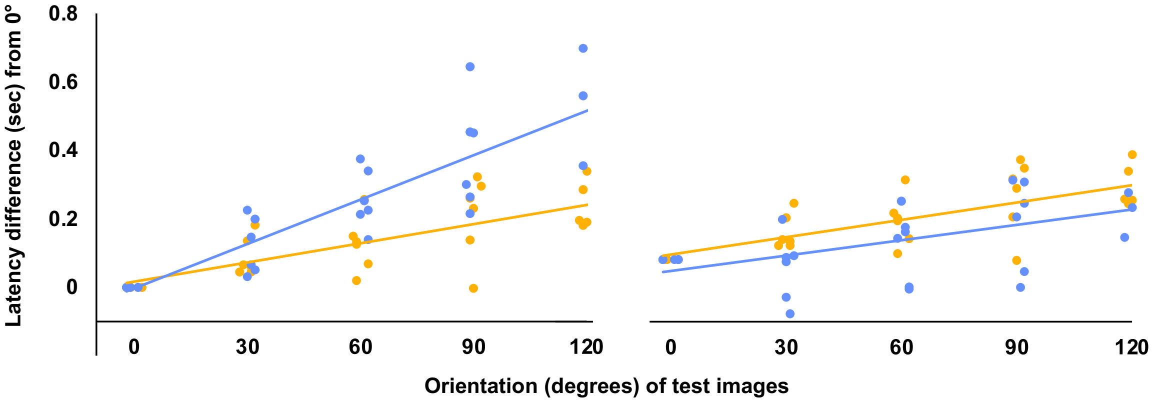

Fig. 3. Left: Response times increased less with rotation on cued (gold) than uncued (blue) trials (Experiment 3 Cued vs Experiment 1). Right: Response times increased equally with rotation on cued (gold) and uncued (blue) trials (Experiment 3). The difference in latency for each rotation from latency at 0°. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

providing converging evidence for the presence of this cognitive process in monkeys. Monkeys matched remembered upright shapes to rotated shapes and showed the hallmark longer response time with greater rotation. Monkeys transformed mental images as instructed by a cue with precision better than 30° in Experiment 2 and may have used this cue to mentally rotate images prior to seeing tests in Experiment 3. Thus, the mental images monkeys formed included fine perceptual details and remained true to physics through substantial transformation. The findings from these three experiments, combined with evidence from studies of blindsight and metacognition that suggest phenomenal visual experience in monkeys (Andersen et al., 2014; Cowey & Stoerig, 1995; Moore et al., 2001), indicate that rhesus monkeys form and manipulate mental images, as defined by the three criteria we defined.

Mental images could underlie a variety of nonhuman animal behaviors. Vervet monkeys make specific anti-predator responses when they hear particular alarm calls and may visualize the predator indicated by the call in support of this specificity (Cheney & Seyfarth, 1990). It is common for animals to form expectations of specific rewards, as shown by selective satiation experiments, and these expectations could involve visualizing the expected food (Baxter & Murray, 2002). While it may be considerably less common for nonhumans to have cause to transform mental images than is the case for humans, tool-users might gain sophistication in their use of tools with the aid of isomorphic transformations of mental images, and navigation might be enhanced by visualization of mental maps (Hunt, 1996; Tolman, 1948; Tomasello, Davis-Dasilva, Camak, & Bard, 1987).

Human mental representations often include propositional linguistic content in addition to, or instead of, recapitulating perceptual processes (Pylyshyn, 1973; Shepard & Cooper, 1982). Lacking language, nonhumans may be especially dependent on representations that are based in the processes that give rise to the initial perception of stimuli, rather than propositional representation. Our findings suggest an evolutionary continuity, at least among primates, in visual imagery. Evidence from other cognitive paradigms suggests that nonverbal animals rely on quasi-visual, rather than propositional, representations to solve a range of tasks including transitive inference (Gazes et al., 2017; Gazes, Chee, & Hampton, 2012), quantity discrimination (Brannon & Merritt, 2011; Gazes et al., 2017; Lourenco & Longo, 2010), and memory for order (Bunsey & Eichenbaum, 1996; Templer & Hampton, 2013). Visual imagery may be an especially powerful form of representation for nonhumans. The evidence presented here showing that monkeys transform mental images may begin to transform our image of monkey mentality.

CRediT authorship contribution statement

Thomas C. Hassett: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Victoria K. Lord:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Robert R. Hampton:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2022.105225.

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