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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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Humans consistently show mental rotation, the spatial ability to rotate images in mind, but other species, such as pigeons, have been reported to employ alternate visual processing strategies. These species differences raise questions about the evolution of mental rotation. Investigation with non-human primates holds promise to answer these questions, but the field is limited thus far. We aimed to fill this gap by testing whether rhesus macaques show evidence of mental rotation. Five rhesus macaques performed a match-to-sample, mirror image-discrimination task with rotated abstract, asymmetrical shapes. The monkeys showed the characteristic mental rotation effect – increasing reaction times and decreasing accuracy at greater angles of rotation. But, performance was at chance for large angles of rotation. We designed a second experiment, with simplified procedures, to facilitate mental rotation. In Experiment 2, monkeys continued to show increasing latency with angle while performing above chance at every angle of rotation. These findings lead us to conclude that rhesus macaques do show evidence of mental rotation. Our results provide some of first support from a non-human primate for the main two evolutionary hypotheses for mental rotation, and these findings should motivate broader investigation of mental rotation in a range of primate and non-primate species.

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Evidence of Mental Rotation in Rhesus Macaques

Cognitive psychologists have extensively studied mental rotation, the ability to transform and rotate an image in mind, over the past few decades. The initial investigation into this spatial ability was performed by Shepard and Metzler in 1971. Human participants had to determine whether two simultaneously presented abstract shapes were the “same”, identical shapes, or “different”, mirror image isomers. When these shapes were presented at increasingly discrepant angles, participants took significantly longer to respond and made more errors. There was a strong linear relationship between reaction time and angle of rotation. These authors interpreted these results as evidence that the subjects were holding one shape in mind and rotating it into congruence with the other to make the comparison. Greater reaction time would result from rotating a greater distance. Introspective reports of the participants supported this interpretation. Based off their work, the characteristic mental rotation effect is now defined as linearly increasing reaction time and decreasing accuracy with increasing angular disparity. Although, some authors have assumed a more liberal definition, arguing that either increased latencies or errors alone qualify as evidence of mental rotation (Delius & Hollard, 1995), and humans are often so accurate that investigators focus on latency (Shepard & Cooper, 1986).

This establishment of objective criteria to measure a transformation of mental images led to the broad investigation of mental rotation in humans. Researchers have tested how the color, texture, complexity, and dimensionality of stimuli influence mental rotation (Bethell-Fox & Shepard, 1988; Cooper, 1975; Corballis, 1997; Shepard & Cooper, 1986). Different procedures, involving simultaneous presentation of shapes, same-different paradigms, match to sample, and pen and paper multiple choice have been employed. These mental rotation tasks have been used to target the manipulation component of working memory, which is responsible for the transformation of information held in mind, dissociable from active maintenance of information, and has been shown to be especially reliant on executive control (Kim et al., 2004; Thakkar & Park, 2010). Psychologists have further used the mental rotation paradigm to investigate the specific cognitive deficits, such as selective impairment of working memory manipulation, of clinical populations: interestingly, Schizophrenic patients have shown spared mental rotation ability while Parkinson's patients show deficits in mental rotations tasks (de Vignemont et al., 2006; Lee et al., 1998: Thakkar & Park, 2010). This large body of research has even related mental rotation performance to spatial IQ, mathematical reasoning ability, and the ability to solve complex engineering or stereochemistry problems (Delius & Hollard, 1995; Shepard & Cooper, 1986). Thus, mental rotation tasks have allowed researchers to understand the range, limit, and relevance of humans' spatial transformation abilities.

The mental rotation effect has been consistenly found in humans over the past few decades, making it evident that humans can rotate images in mind and likely do so to solve a number of spatial problems. But, this cognitive strategy of rotation is both time consuming and cognitively demanding. A perceptual processing strategy that allows immediate discrimination and recognition of an object at any orientation, without needing to rotate, would save an animal time (Delius & Hollard, 1995). The field has begun to ask whether humans have lost such an efficient processing ability or whether mental rotation provides some advantage by permitting imagined rotations (Delius & Hollard, 1995; Shepard & Cooper, 1986). Understanding the role of mental rotation in human cognition may be aided by answering questions as to when and why this spatial ability evolved. Comparative studies of mental rotation will illuminate the degree to which species differ in this transformation ability and, more importantly, shed light on the evolution of mental rotation. Mental rotation research in animals may even permit the use of animal models in the future to study the nature of specific cognitive deficits seen in clinical populations, such as those noted with Schizophrenic patients (Thakkar & Park, 2010). Investigation of mental rotation in nonhuman animals holds great promise for these reasons, however there has been a paucity of animal research to date.

Delius and Hollard (1995), following investigation of mental rotation in pigeons, proposed the first hypothesis for the evolution of mental rotation. A short review of their findings is helpful to understand their argument. When pigeons performed a simultaneous match-to-sample (MTS) mirror-image discrimination task, their reaction time was independent of the angular rotation of stimuli. It was assumed that pigeons understood the task, as they performed above chance. The authors named this processing strategy rotational invariance because the pigeons' performance did not vary with rotation. When humans were given the exact same task, they validated the paradigm and showed the expected increasing linear dependence of reaction time on angular disparity. In follow-up experiments, the pigeons continued to show rotational invariance across a delay, with unfamiliar shapes, and when the sample was rotated instead of the comparison stimuli. This was clear evidence of divergent processing strategies in the two species.

To explain the differences between pigeons and humans, Delius and Hollard (1995) suggested that the species face different environmental pressures and perceive the world under different constraints. They propose that these ecological constraints influence how species process information and have likely led to the evolution of different processing systems. Specifically, birds see objects in a variety of orientations while feeding and flying and rely on a horizontal reference frame of the horizon (Lohmann et al., 1988). In their 3D rich environment, it is beneficial to recognize objects quickly in any orientation. While this rotational invariance strategy is more efficient than mental rotation, it is costly in neural processing (Delius & Hollard, 1995). Humans may have lost this efficient but costly processing ability due to the development of an upright gait, as most visual processing is done on objects in a fixed orientation due to gravity (Delius & Hollard, 1995; Kohler et al., 2005; Parr & Heintz, 2008). These authors argue that humans and pigeons developed different visual processing systems because of differences in how they perceive and experience the world. This ecological hypothesis broadly predicts that arboreal species would show rotational invariance, while more terrestrial species would show mental rotation.Yet, it is worth nothing pigeons spend a great deal of time upright, like humans, while foraging for food. The visual processing demands placed on humans and piegons may be more similar than these authors purport. The ecological hypothesis, therefore, it not entirely convincing and merits further investigation.

Further animal work has begun to evaluate this widely discussed hypothesis. Mauck and Dehnhardt (1997) tested mental rotation in a sea lion using a delayed match-to-sample task with mirror-image discrimination. They hypothesized that the sea lion would show rotational invariance because sea lions have similar visual ecological demands as birds: both rely on a horizontal reference frame, either the surface of the water or horizon. To their surprise, the sea lion showed strong evidence of mental rotation. They conclude that use of a horizontal reference frame does not necessarily lead to rotational invariance, as Hollard and Delius (1995) proposed. However, one could argue that these findings could be partially explained by the fact that sea lions are pinnipeds. Pinnipeds – semi-aquatic marine mammals - descended from terrestrial ancestors and returned to the aquatic environment millions of years ago (Uhen, 2007). It is possible that sea lions show mental rotation due to their ancestors’ adaption to terrestrial living.

It is therefore problematic to conclude whether these findings with a sea lion challenge or support the ecological hypothesis.

Another hypothesis regarding the evolution of mental rotation, which we call the motor planning hypothesis, proposes that mental rotation was not the byproduct of losing an efficient visual processing strategy. Instead, it manifested in tandem with more sophisticated visual cognitive abilities. Wohlchlager and Wohlshlager (1998) suggest that mental rotation is more related to actively planning rotations, a high level cognitive process, than the imagined perception of motion, a low level cognitive process. Specifically, a number of investigators have proposed that the evolution of mental rotation coincided with primates gaining the use of free hands and manipulating objects (Burmann et al., 2005; Wexler et al., 1998). Mental rotation may have allowed humans to try out physical transformations and manual rotations of objects before actually performing them (Shepard & Cooper, 1986). This ability may save an animal time and effort, as they are able to evaluate the outcome of these movements in advance. This hypothesis is supported by the strong connection between physical and mental rotation: mental rotation consistently activates key brain areas related to motor action planning; motor processes can facilitate mental rotation (Wexler et al., 1998); performing simultaneous physical rotations and mental rotations in opposite direction causes interference (Wohlschlager & Wohlschlarger, 1998); and training on motor coordination activities increases mental rotation performance (Jansen et al., 2011). So, this hypothesis predicts that species that perform object manipulations and tool use should show evidence of mental rotation. This could account for why pigeons, who do not have hands allowing rotations of objects, would not have evolved mental rotation. But, the finding that sea lions, who similarly do not have hands, show mental rotation challenges this reasoning.

While these hypotheses offer interesting explanations for the differences in mental rotation ability and processing strategies across species, they have not yet sufficiently explained the results of early animal work. The ecological hypothesis has suffered from the fact that very few nonhuman species have actually been tested on mental rotation, and the motor planning hypothesis has barely been discussed in animal work. Further, the findings with the sea lion raise questions about the validity of both the ecological hypothesis and motor planning hypothesis. It is too early to make definitive conclusions about the evolution of mental rotation and there is a need for investigation in more species.

Comparative work with non-human primates, our close evolutionary ancestors, holds promise to help uncover the evolutionary picture. Non-human primates show adaptive radiation from arboreal ancestors and now inhabit a range of arboreal and terrestrial habitats (Eppley et al., 2016; Singh et al., 2001; Wells & Turnquist, 2001). Filling these different ecological niches has influenced their anatomical and, likely, cognitive evolution (Eppley et al., 2016). Primate species also vary with respect to their extent and complexity of tool use and object manipulation (Torigoe, 1985). Thus, studying mental rotation in non-human primates may allow the field to evaluate the validity of the aforementioned evolutionary hypotheses.

To date, only a limited number of mental rotation studies have been conducted using non-human primate species, and thus, it is not yet possible to make strong conclusions about the extent of this cognitive ability in monkeys. Of the limited research that has been conducted, most studies have tested very few subjects or used shapes and procedures that are inconsistent with the standards implemented in human research. Brief reviews of the findings thus far will elucidate these inconsistencies.

Vauclair et al. (1993) performed some of the earliest nonhuman primate work, with a mental rotation task involving unilateral presentation of stimuli. They reported a cognitive lateralization for mental rotation in baboons, such that baboons showed mental rotation only for images presented to the right visual field. When their paradigm was tested with humans, the participants showed mental rotation regardless of which hemisphere stimuli were presented to. Comparison of results between species also revealed large differences in mental rotation rate: baboons were twice as fast as humans. These results must be interpreted with caution. First, this difference in rate of rotation causes some concern, as other studies have found similar rotation rates for monkeys and humans in mental rotation tasks (Georgopolous & Pellizzer, 1995). Second, the author included only two stimuli, an F and P. This very small set size that may have promoted the memorization of shapes at each angle and, maybe more importantly, humans have much greater familiarity with these stimuli. It has been shown that humans are able to represent and rotate familiar shapes more easily than unfamiliar shapes (Bethell-Fox & Shepard, 1988). The humans had greater accuracy than the monkeys, so these shapes may have aided humans in rotations but provided no comparable benefit to the baboons. Given these factors, definitive conclusions about baboons' mental rotation abilities or strong comparisons between species cannot be made.

In line with the ecological hypothesis discussed above, Burmann et al. (2005) hypothesized that a lion-tailed macaque, a mainly arboreal primate in a three-dimensionally rich environment, would show rotational invariance. But, the monkey's performance on a two-alternative match-to-sample mental rotation task suggested neither rotational invariance nor mental rotation: error rates and reaction times were greater on rotation than non-rotation trials, but they did not monotonically increase with the magnitude of the angle. The researchers proposed that the lion-tailed macaque is an intermediate in the evolution of mental rotation. The possibility of macaques being an evolutionary intermediate is interesting, but their findings are not convincing as they only tested a single monkey. Considering the large variation in humans' performance in mental rotation tasks, we are hesitant to make conclusions about an entire species from one subject (Cooper and Shepard, 1973).

Of particular interest to our work are the few studies conducted with rhesus macaques. Nekovarova et al. (2012) used spatial maps to compare the mental transformation abilities of rhesus macaques and humans. They found that the humans were able to perform both mental translocations – shifts in the x and y direction - and rotations of spatial maps. The monkeys were only able to perform translocations, not rotations. But, this was a comparison of over fifty human subjects to only two rhesus macaques. Their design also drastically differed from the commonly implemented mental rotation tasks. Subjects were required to remember the location of a circle on a spatial map rather than discriminate shape identity. This is a crucial difference, considering that mental rotation has been shown to cause bidirectional interference in object, but not spatial, working memory tasks (Hyun & Luck, 2007). In addition, their measure of performance was anomalous with respect to previously established conventions. They recorded the number of locations touched on the map before the correct answer was chosen. This measurement is related to error rates, but they made no attempt to measure latency. These methodological and measurement differences make it difficult to interpret their findings within the current field of literature.

A study more similar to what has been used in other animals and humans was performed by Parr and Heintz (2008), who tested five rhesus macaques with a match to sample, mental rotation task. They presented houses, conspecific faces, or nonconspecific faces as stimuli in a variety of orientations. Because the monkeys' performance decreased linearly as rotation angle increased for all three types of stimuli, the authors concluded that the monkeys were rotating stimuli to the upright position for processing. However, these results are problematic as there was no measurement of reaction time and it has been noted that latency is the critical measurement in mental rotation tasks (Shepard & Cooper, 1986). In addition, their choice of stimuli also varies from the field's standard of using mirror images as comparison shapes.

The strongest evidence of mental rotation in rhesus macaques comes from neural recordings performed by Georgopoulus et al. (1989). These authors conducted single cell recordings in the motor cortex while two rhesus macaques performed a visuomotor mental rotation task. They found that the imagined motion population vector linearly rotated in time towards the intended movement. Crucially, the rotation of the vector, calculated from activity of cell assemblies, occurred before rotation. These authors later argue that this sequential activation of cells is evidence for a directional transformation and, therefore, for mental rotation in macaques (Georgopoulus et al., 1995). While this task involved rotation of a movement vector rather than shape, later studies have shown similar processing rates for visuomotor and visual mental rotations in humans (Pellizer & Georgopoulus, 1993; Wohlschlager & Wohlschlager, 1998).

Finally, Kohler et al. (2005) conducted the study most in accordance with the methods used with humans. But, they reported inconclusive findings. These authors predicted that rhesus macaques would show evidence of mental rotation, as they are a primarily terrestrial primate species. They ran three monkeys on a mirror-image discrimination, match-to-sample mental rotation task. Two monkeys did not show evidence of mental rotation: they showed an increase in error rates, but not reaction times, with angular disparity. The third monkey performed in a manner consistent with mental rotation, as he showed a significant increase in reaction time and increase, though non-significant, of error rates with angular disparity. The researchers suggest that two different processing systems, rotational invariance and mental rotation, may coexist within a species. This is the first mention of a single species showing both types of visual processing and merits further investigation into mental rotation of rhesus macaques.

In summary, the literature to date on mental rotation in non-human primates is both inconsistent and inconclusive. The studies performed have used very few subjects and have often lacked the procedures to appropriately determine if monkeys mentally rotate. Researchers have omitted latency measurements, used arbitrarily different shapes instead of mirror images, or designed tasks with largely different demands than typically used with humans. Due to these limitations, strong conclusions can not yet be made about mental rotation in non-human primates. Thus, there is a need within monkey research to conduct experiments with larger sample sizes and with appropriate procedures to adequately address this topic.

Experiment 1

In the current study, we tested whether rhesus macaques show mental rotation. We were able to test and analyze data from a larger group of non-human primates than any study thus far. Larger sample sizes are especially beneficial in mental rotation research, given the large individual variation of mental rotation rate found in human research (Shepard & Cooper, 1986). Our experiment is designed with methods very similar to the original mental rotation experiments in humans, with consideration of those aspects best suited to animal testing from previous work (Cooper & Shepard 1973; Delius & Hollard, 1995; Kohler et al., 2005). The task was programmed as a match-to-sample, mirror-image discrimination paradigm. This involves a delayed matching task, in which the monkey must match a previously presented sample with one of two rotated comparison stimuli.

The comparison stimuli presented at test were always mirror isomers of each other. A number of researchers have attested that this is essential to test for mental rotation (Delius & Hollard, 1995; Shepard & Metzler, 1971). This design prevents subjects from solving the discrimination based on local feature differences of the shapes, as both a shape and its mirror image have the same features (Cooper & Shepard, 1973; Tarr & Pinker, 1989). In addition, humans often perform mental rotations to made mirror discriminations but may not need to rotate to discriminate arbitrary shapes (Cohen & Kubovy, 1993; Delius & Hollard, 1995). Though some research has previously shown mirror-image equivalence in monkeys, a number of studies have found that monkeys are capable of learning and performing mirror-image discriminations (Burmann et al., 2005; Kohler et al., 2005: Vauclair et al., 1993).

We included rotations in intervals of 30 degrees up to 120 degrees. We did not include 180° as a possible rotation value, as some studies with humans have found that the reaction time for this angle deviates from the linear function (Shepard and Cooper, 1986). It is probable that subjects are employing a strategy other than rotation, such as flipping, to complete trials with an orientation of 180° (Cooper & Shepard, 1973; Hamm et al., 1997). Due to the ambiguity of the strategy that participants employ at this angle, our design included rotations up to 120°.

We implemented stringent qualifications to conclude that monkeys are mentally rotating, necessitating that both reaction time and error rates increase with angular disparity. Shepard and Cooper (1986) note that the critical measurement in mental rotation is latency. But, animal work often measures error rates as well because animals typically show lower accuracy than humans in challenging memory tasks (Elmore & Wright, 2015). Due to this variation in accuracy, animals may show increasing error rates with angle in addition to increasing latency. We hypothesize that if monkeys use a mental rotation strategy to solve rotated mirror image discrimination tasks, then they will show increasing error rates and reaction times with increasing angle of rotation.

Method

Subjects

Five male adult rhesus monkeys (*M. mulatta*) of mean age 9.8 years were used. Monkeys were individually housed, but had auditory and visual contact with conspecifics in the room. Monkeys were given ad libitum access to water. Monkeys received their daily caloric intake through a combination of nutritionally balanced pellets and chow. All monkeys had prior experience with computerized cognitive MTS tasks. The monkeys were tested for seven hours, six days a week, and all testing was voluntary.

Apparatus

Each morning, a computer rig testing apparatus was hung on each monkey's home cage. The apparatus consisted of a touch-sensitive LCD monitor (Elo TouchSystems, Menlo Park, Ca), two food dispensers (Med Associates Inc., St. Albans, VT), and speakers. This allowed delivery of reinforcement in both food and auditory form. Specific testing software was programmed using Visual Basic.

Procedure

Monkeys performed a match-to-sample, mirror-image discrimination task with rotated images. The procedural steps for a non-rotation and rotation trial are shown in Figure 2. The task began with presentation of a green start square on the screen. When the monkey touched the start square twice, a sample shape was immediately presented. Once the monkey touched the sample shape twice, a brief 500-millisecond delay occurred and the two comparison stimuli appeared side by side. One of these two stimuli was the previously presented sample and the other was its mirror image. The monkey had to choose which of these two stimuli matched the sample that had been previously shown upright. Each shape and its mirror image could appear as the sample and therefore be the correct answer at test. This prevented the monkeys from solving the discrimination based on rote memorization of one version of the shape that was always correct. The side of the screen on which the correct answer was presented was counterbalanced and pseudo-randomized across trials. We measured reaction time by timing the passage of time from when the comparison stimuli appeared on the screen to when the monkey made a choice. Correct choices were followed by an immediate food reward, a positive auditory reinforcing sound, and a 3 second inter-trial interval (ITI). Incorrect choices were followed by negative auditory reinforcement and a 6 second time-out. The screen during the ITI and the time-out was black. Latency to touch the green start square, sample, and test image was collected on every trial.

Training consisted of three phases. For all three phases, monkeys needed to get at least 80% of trials correct within a given session, for two consecutive sessions, in order to progress to the next training phase. In the first phase, comparison stimuli always appeared at 0° to ensure that the monkeys could perform mirror image discriminations. In the second phase, comparison stimuli could appear at 0°, 30°, or 90°. The last training phase included presentation of stimuli at 0°, 30°, 60°, 90°, or 120°. Following completion of the last training phase, monkeys entered a testing phase, where eight novel shapes and their mirror images were used as image stimuli. Monkeys first completed trials with these eight novel shapes shown only at the upright orientation. They had to reach learning criterion 0° before rotations were introduced, which ensured that the monkeys could discriminate between these novel shapes and their mirror images. After reaching criterion at 0°, comparison stimuli during test could appear at 0°, 30°, 60°, 90°, or 120° in either the clockwise or counterclockwise direction.

Each session consisted of 80 trials. The number of sessions during training phases was determined by the learning criterion. During test, the monkeys performed twenty sessions. In each session, each stimulus and its mirror image were presented as samples and was the correct choice at each angular orientation.

Data Analysis

Latency and accuracy of the monkeys was analyzed. Only latency for correct trials was included in the analysis, as it is unclear what mental strategy or process leads to an incorrect answer (Burmann et al, 2005). Accuracy is reported as proportion correct, and these scores for each monkey at each angle were arcsine transformed in order to normalize the data distribution.

Statistical tests were performed for the final twenty sessions of training data and the twenty sessions of test data. Analysis of training data was included because, at the end of training, monkeys were completing the task with relatively familiar shapes but, at test, with relatively novel shapes. Comparison of these two sets of data allowed evaluation of how well the monkeys had generalized what they had learned during training to relatively new shapes. We performed two repeated measures ANOVAs to determine whether the mean accuracy and latency of the monkeys varied as a function of angle. Post-hoc pair-wise comparison tests were also performed to evaluate the differences in accuracy and latency between every possible pair of angles. A binomial probability test was performed to determine that, within the block of 20 sessions analyzed, monkeys needed to get at least 176 out of 320 possible trials correct at each angle to be performing above chance. Group averages for number of trials correct at each angle were compared to this value to determine if the monkeys were performing significantly above chance at each angle, during both test and training. In addition, performance during test and training was compared in order to evaluate the degree to which angle and stimulus familiarity influenced accuracy and latency. Two repeated measures ANOVAs were run to evaluate latency and accuracy, with the levels of test and training, across angles.

Results

Five monkeys completed the three phases of training and a testing phase. The five monkeys took an average of 62.6 sessions to reach criterion for training phase 1, thus confirming that they were able to perform mirror-image discriminations with abstract shapes. Monkeys required an average of 232 sessions to reach criterion for training phase 2. Only one of the five monkeys reached criterion for training phase 3. Three monkeys had achieved two consecutive sessions with at least 70% of trials correct. The binomial test revealed that the fifth monkey was performing above chance at every angle ($p<0.05$), except for at 120 degrees ($p>0.05$). Given that these four monkeys' accuracy and latency at each angle were not significantly improving across the hundreds of sessions of training, these performance levels were considered sufficient to progress monkeys to the test phase. The monkeys had completed an average of 224.2 in this final training phase before moving to test

Group averages at the end of training for accuracy across the angles of rotation are plotted in Figure 3 and group averages for latency at the end of training are plotted in Figure 4. A significant main effect of angle on accuracy was found ($F(4,16)=36.318$, $p<0.001$), such that monkeys had lower accuracy at larger angles of rotations. Pairwise comparisons tests revealed significant differences in accuracy between all pairs of angles ($p<0.05$), except for accuracy between 60°/90° and 90°/120° ($p>0.05$). There was also a significant main effect of angle of latency ($F(4,16)=30.976$, $p<0.001$). Monkeys' latency increased as the angle of rotation increased. All pair-wise comparisons were significant for reaction time across angles ($p<0.05$). Therefore, at the end of training, monkeys showed evidence of the mental rotation effect: their accuracy decreased and latency increased with increasing angle of rotation. Monkeys' accuracy was significantly above chance at every angle ($p<0.05$), except at 120° ($p=0.052$). It is possible that that the monkeys showed the lowest accuracy and longest reaction time at 120° due to a strategy of guessing. But , given that accuracy was above chance for all other angles of rotation, monkeys' performance at the end of training does provide evidence for mental rotation.

Mean accuracy at test is plotted against angle in Figure 5 and mean latency at test is plotted against angle in Figure 6. There was again a significant main effect of angle on accuracy ($F(4,16)=49.940$, $p<0.001$), such that monkeys had lower accuracy at larger angles. There were significant differences in accuracy for each pair of angles ($p<0.05$), except for accuracy between 90°/120° when the monkeys were performing at chance level. There was also again a significant main effect of angle on latency ($F(4,16)=30.876$, $p<0.001$), with monkeys taking longer to respond at larger angles of rotation. The pairwise comparisons revealed significant differences in latency between all pairs of angles ($p<0.05$), except between 60°/90° and 90°/120° angles ($p>0.05$). At larger angles of rotation, monkeys took about the same amount of time to choose a comparison stimulus. These results show that as the angle of rotation increased, the monkeys' accuracy decreased and latency increased. But, the differences in reaction time and accuracy diminished at larger angles. At test, monkeys' accuracy was significantly above chance for the smaller angles of 0°, 30°, and 60° ($p<0.05$) but not significantly above chance for the larger angles of 90° and 120° ($p>0.05$). Thus, at test the monkeys were performing at chance for a greater number of angles than at the end of training. Monkeys' near chance performance at larger angles makes us cautious in concluding that the monkeys were rotating at test.

Comparison of Training and Test Performance

The analysis of accuracy revealed that there was no significant main effect of stimulus familiarity ($F(1,4)=6.213$, $p=0.067$) and no significant interaction ($F(4,16)=2.059$, $p=0.134$). There was a significant main effect of angle on accuracy ($F(4,16)=73.363$, $p<0.001$). Overall, accuracy was significantly different across the angles and decreased with greater angles of rotation. But, monkeys' performance did not depend on whether the monkeys were rotating familiar or relatively novel shapes. In the analysis of latency, there was again no significant main effect of stimulus familiarity ($F(1,4)=0.442$, $p<0.001$) and no significant interaction ($F(4,16)=2.528$, $p=0.081$). There was a significant effect of angle on latency ($F(4,16) = 34.663$, $p<0.001$). Similar to accuracy, monkey's reaction times were significantly different across angles but did not differ depending on whether they were in the testing or training phase.

Individual analysis of test and training data individually had suggested that monkeys' performance at test was lower than during training: monkeys' accuracy was at chance for a greater number of angles than at the end of training and the latency was not significantly different between the largest angle pairs. But, direct comparison with repeated measure ANOVAs showed that monkeys' performance was comparable at the end of training, when presented with highly familiar shapes, and test, when presented with novel stimuli. In both cases, performance was lower at larger angles of rotation.

Discussion

Our results from Experiment 1 provide evidence that rhesus macaques are able to mentally rotate. At the end of training and at test, monkeys' reaction times increased and accuracy decreased with increasing angles of rotation. This pattern of results matches the mental rotation effect originally defined by Shepard and Metzler (1971). These findings support our hypothesis that rhesus macaques use a mental rotation strategy to solve rotated mirror-image discrimination tasks.

While our monkeys did show the characteristic mental rotation effect of angle on accuracy and latency, performance was low at large angles of rotation. Accuracy was at chance for the largest angle at the end of training and, at test, accuracy fell to chance for both 90° and 120°. This dip in performance is problematic for our interpretation of the effect of angle on latency. It is possible that longer reaction times at larger angles resulted from monkeys guessing at large angles of rotation. This strategy could create the increasing linear latency function if it took the monkey longer to give up and guess at large angles than to accurately rotate at small angles. The monkeys' low performance at large angles makes us hesitant to confidently conclude that monkeys were mentally rotating shapes presented at every angle.

Our monkeys' low accuracy at large angles of rotation may be due to the overall difficulty of our task. With the additional cognitive effort required by greater rotations, the task may have become exceedingly difficult at the largest angles. Thus, this very high level of difficulty may have prevented monkeys from accurately rotating and discriminating specifically at large angles of rotation. The task was originally designed to be in close accordance with human work, but some aspects of the design may have been especially difficult for our monkeys.

First, the abstract, asymmetrical shapes presented were very complex and it may have been difficult to form holistic mental representations of them. A number of studies have shown that human mental rotation rate is slower with complex shapes, and it has been suggested that mental rotation is limited to shapes that can be represented holistically (Cooper, 1975; Corballis, 1997). Bethell-Fox and Shepard (1988) directly tested the effect of stimulus complexity on mental rotation. Their subjects were originally much slower at rotating complex matrices compared to simple matrices. When the subjects were given practice with the complex matrices, the effect of complexity on rotation rate disappeared. These authors suggest that when complex stimuli become familiar, they can be represented holistically and transformed by rotation. When complex stimuli are unfamiliar, subjects may have to engage in less efficient piece-meal rotation. Our monkeys may have been unable to represent our complex shapes holistically and perform rotations with them, especially when relatively novel shapes were introduced at test. The monkeys may have instead been forced to rotate the shapes in a less-accurate, piece-meal fashion. This strategy would take more time than holistic rotation, which may have led to decay of the memory trace of the sample and, thus, to monkeys guessing. Bethell-Fox and Shepard's (1988) findings do suggest that continued practice on these complex shapes may promote accurate, holistic rotations in our monkeys.

The difficulty of our task may have been exacerbated by the fact that comparison shapes were rotated in either a clockwise or counterclockwise direction. The task was originally designed in this manner mimicking both human and animal work (Burmann et al., 2005; Cooper, 1975; Kohler et al., 2005; Tarr & Pinker, 1989). Tarr and Pinker (1989) note that the human research has found that subjects have equivalent reaction times for rotations in both clockwise and counterclockwise directions and that subjects typically rotate in the direction of the shortest path to upright. Given the inability to give verbal instructions to our monkeys, this design may have been too difficult. The direction in which comparison stimuli were rotated was never cued, and thus, monkeys needed to guess which direction to mentally rotate the sample. Because clockwise and counterclockwise rotations appeared equally across all rotation trials, monkeys may have mentally rotated in the wrong direction on close to half of the trials. Wohlschlager and Wohlschlager (1998) suggest that humans may also sometimes rotate in the wrong direction (i.e. along the longer path to achieve congruence between shapes) when shapes are presented at angles close to 180 degrees. Thus, this ambiguity may have influenced our monkeys' performance the most at the angles furthest from upright. A significant amount of time spent rotating in the wrong direction may have caused a monkey to give up and randomly guess. Or, the monkey may have then attempted to rotate the image the other direction. Given the length of time this process would take, the mental image strength likely decayed and may have been too weak to find a match.

Our findings from Experiment 1 lead us to believe that our monkeys are capable of mental rotation. The five rhesus macaques showed indication of mental rotation at the end of training and during test. We believe that low performance at large angles of rotation was due to the overall difficulty of the task. In order to strengthen our conclusion that our monkeys were engaging in mental rotation, we performed a follow-up experiment with simplified methods. We aimed to show the characteristic mental rotation effect while having the monkeys' performance significantly above chance at every angle. This would eliminate the possibility that the effect of angle on accuracy on latency found in Experiment 1 was attributable to the monkeys' guessing at larger angles, and thus, would provide a more convincing demonstration of mental rotation in non-human primates.

Experiment 2

A second experiment was designed to facilitate mental rotation, with the goal of replicating our initial findings under conditions that are a more robust test of the mental rotation hypothesis. Two aspects of our initial design may have been exceedingly difficult and prevented the monkeys from accurately rotating shapes at all orientations presented. First, in the previous experiment the comparison stimuli could appear at rotations in either the clockwise or counterclockwise direction, and monkeys were provided no cue to signal which direction to rotate. This ambiguity may have led to confusion, guessing, or decay of the memory trace if monkeys took the time to rotate in the wrong direction. Monkeys may have been most likely to begin rotating in the wrong direction for angles furthest from the upright, therefore causing decrements in performance especially at large angle of rotation. To simplify the task, Experiment 2 was designed such that monkeys rotated stimuli in only one direction. The comparison stimuli were now always presented at a rotation of 0°, 30°, 60°, 90°, or 120° in only the clockwise direction. Previous animal work has used similar procedures by restricting the rotation of stimuli to one direction (Delius & Hollard, 1995; Parr & Heintz, 2008). This should simplify the task for the monkeys, as they will not have to guess which way to begin rotating an image.

To further simplify the procedure, monkeys were presented with familiar shapes to help promote holistic rotations of our complex stimuli. Five of the eight training shapes from Experiment 1, with which the monkeys already had extensive practice, were used in Experiment 2. A possible concern with re-using these shapes would be that the monkeys may form a representation of each shape at the trained orientations (Cooper, 1975; Tarr & Pinker, 1989). Using this strategy, monkeys could perform successfully by searching a mental table of memorized shapes for the correct answer instead of rotating a shape in mind (Georgopoulus & Pellizzer, 1995). However, it is unlikely that monkeys used a bank of memorized shapes because this strategy would have produced a flat-line function between latency and angular disparity (Cooper, 1975). The time to respond at each angle of rotation would have been equivalent across angles and only dependent on the time to mentally search for the correct answer (Tarr & Pinker, 1989). Our data from end of training in Experiment 1 do not support this possibility. After hundreds of sessions with the set of eight training stimuli, monkeys' latency was significantly different at each angle and there was still an increasing linear function between reaction time and angle. Because monkeys did not show evidence of forming multiple representations with training stimuli, we believe it is valid to re-use these shapes. We anticipate that increasing the familiarity of our complex shapes will make it easier for our monkeys to perform accurate, holistic rotations.

We predicted that the methodological changes made in Experiment 2 would facilitate mental rotation in our rhesus macaques and improve their performance, especially at large angles that require the greatest amount of rotation. We hypothesize that if monkeys perform a match-to-sample, mirror image discrimination task with familiar shapes and with rotations in only one direction, they will continue to show increasing latency with increasing angle of rotation and will show increased accuracy.

Method

Subjects

Six male adult rhesus monkeys (*M. mulatta*) - the five tested in Experiment 1 and one additional monkey - were tested in Experiment 2. Only four monkeys had reached criterion by the time this paper was written, and thus, only the data from these four monkeys is considered. Monkeys' housing, diet, and testing schedules were the same as the previous experiment.

Apparatus

The same computer rig apparatus from Experiment 1 was used.

Stimuli

Five of the eight abstract, asymmetrical shapes used for training in Experiment 1 were randomly chosen and used in Experiment 2. As in the previous experiment, each shape and its mirror image were presented as samples, such that there were 10 possible stimuli presented as samples. The sample shape was always presented at 0°. Comparison images included both forms of each shape, that which was previously presented and its mirror image. The comparison images were presented at 0°, 30°, 60°, 90°, or 120° degrees in only the clockwise direction.

Procedure

Monkeys performed a similar match-to-sample, mirror-image discrimination task with rotated mirror images. The presentation of shapes, comparison stimuli, reinforcement, and measurement of reaction time were the same as the previous experiment.

In Experiment 1, the five angles were introduced progressively across multiple training phases. In Experiment 2, there were no distinct training phases, because the monkeys were already familiar with the shapes and the angles. Comparison stimuli could be presented at 0°, 30°, 60°, 90°, or 120° as soon as the task began. Sessions consisted of 50 trials. In each session, each of the five shapes and its mirror image were presented as samples and was the correct choice at each angular orientation. Furthermore, each angle type was presented equally often within each session.

Data Analysis

Latency and accuracy measurements were the same as in Experiment 1. Additionally, the same statistical tests were performed. Given that there were no training phases in Experiment 2, there was no comparison of test and training data. Performance of the monkeys was now averaged across blocks of five sessions. A binomial test was used to determine that monkeys' performance needed to be above 64% for all angle types within a given block to be considered significantly above chance. The monkeys needed to complete at least twenty sessions overall, with accuracy above 64% at each angle for the final ten sessions. Due to this criterion, additional tests were not run to evaluate if accuracy was above chance. Performance during these final ten sessions were analyzed.

Results

Analysis included the final ten test sessions of the four monkeys who had reached criterion at the time of this paper. These monkeys took an average of 37.5 sessions to reach criterion at each angle. Group averages for accuracy across the angles of rotation are plotted in Figure 7 and group averages for latency across the angles of rotation are plotted in Figure 8. A significant main effect of angle on accuracy was found ($F(4,12)=6.202$, $p=0.006$), such that accuracy decreased at larger angles of rotations. Post-hoc pairwise comparisons revealed that there were only significant differences in accuracy between 0°/90°, 0°/120°, and 60°/120° ($p<0.05$). Accuracy was high and nearly equivalent for small angles of rotation (0°, 30°, 60°).

There was also a significant main effect of angle on reaction time ($F(4,12)=21.837$, $p<0.001$). Latency increased at greater angles of rotation. The pairwise comparisons revealed significant differences in latency between non-adjacent angles (i.e. 0° and 60°) ($p<0.05$), but no significant differences in latency between adjacent angles (i.e. 0° and 30°) ($p>0.05$). While there was not a significant difference in reaction time between adjacent pairs of angles, reaction time always increased as the angle of rotation increased. Figure 7 shows that there was still a clear increasing linear function between angle and latency. These results suggest that monkeys showed a strong mental rotation effect during Experiment 2, while performing above chance at every angle.

Discussion

The results from Experiment 2 support our hypothesis that simplifying the procedures from Experiment 1 would facilitate mental rotation. To address monkeys' poor performance at large angles in Experiment 1, we modified the task such that monkeys were shown familiar stimuli with rotations in a single direction. With these procedural changes, monkeys performed above chance at every angle and showed the characteristic mental rotation effect. Thus, we replicated our initial findings under conditions that were a more robust test of mental rotation.

The pairwise comparisons of accuracy between angle pairs yielded an interesting result. Accuracy was high and similar between small angle pairs and only decreased at the largest angles of rotation. While previous animal work has reported increasing error rates with increasing angle of rotation (Kohler et al., 2005; Parr & Heintz, 2008), high and equivalent accuracy across angles is a hallmark of human mental rotation performance (Shepard & Cooper, 1986). Elmore and Wright (2015) have noted that animals, including rhesus macaques, often have low accuracy at first on challenging visuospatial working memory tasks. However, the authors note that monkeys' performance can be stabilized to a comparative level to humans with continual training. Our monkeys, therefore, seem to be getting much better at the task with continued practice and have begun to show performance more similar to humans.

Our findings from Experiment 2 strengthen our conclusion from Experiment 1 that rhesus macaques, similar to humans, employ mental rotation to solve mirror image discrimination tasks. Given that the monkeys were performing above chance at every angle, the effect of angle on accuracy and latency is likely not attributable to guessing. Thus, our results from Experiment 2 are a convincing demonstration of mental rotation in a rhesus macaque.

General Discussion

Our findings are exciting given the inconclusive findings that have characterized the field of animal mental rotation research thus far. We were able to test and provide evidence of mental rotation in the largest sample of non-human primates to date. All five rhesus macaques met criteria for the mental rotation effect in Experiment 1, evidenced by increasing reaction time and error rates with increasing angular disparity. In a second experiment with a simplified procedure, four monkeys showed the mental rotation effect while performing above chance at every angle. Experiment 2, therefore, provides strong evidence of mental rotation in a non-human primate species. Our design adhered to methods and stimuli similar to the human work with some accommodations for the nature of animal testing. While we did not run our task with humans, this consistency in stimuli and methods may allow strong comparisons of visual cognitive abilities between species in the future.

The conclusion that rhesus macaques have the ability to mentally rotate offers insight into the evolutionary hypotheses that have been proposed for mental rotation. Our findings that rhesus macaques, a terrestrial primate species, show evidence of mental rotation provides support for the ecological hypothesis. This hypothesis would explain that rhesus macaques do not show the efficient ability to discriminate and recognize objects at any orientation, as they spend a majority of their time on the ground. They perceive objects in a fixed orientation bound by gravity, and thus, there is not a strong selective pressure for the costly rotational invariance strategy (Delius & Hollard, 1995). Kohler et al. (2005) hypothesized that the three rhesus macaques they tested would show mental rotation for this reason, but the authors reported inconclusive results. The case study with a single lion-tailed macaque, an arboreal species, did not find strong support for or against this hypothesis: the monkey showed a strategy in between mental rotation and rotational invariance (Burmann et al., 2005). Therefore, our study is the first study to date with macaques that provides strong support for the ecological hypothesis.

Our results also support the motor planning hypothesis, which argues that the ability to mentally rotate images evolved because it provided a mechanism to try out physical rotations in advance. This ability would be most beneficial in species like humans, who manipulate advanced tools and build complex structures, but would also be beneficial in species with more limited tool use (Shepard & Cooper, 1986). Macaques may be such a species, as they show a variety of object manipulations and perform some tool use (Hihara et al., 2003; Torijoe, 1985). Mental rotation may have evolved in rhesus macaques as it saved them time and effort by allowing them to plan these manual rotations. This motor planning hypothesis has rarely been discussed in the animal work. Thus, our study contributes to this hypothesis by finding some of the first evidence of a non-human species that performs object manipulations and shows mental rotations. Future studies could directly test this link by modelling studies after some of the human work: investigating monkeys' performance while performing simultaneous mental and manual rotations (Wexler et al., 1998) or investigating if practice with motor coordination tasks improves mental rotation performance (Jansen et al., 2011).

While our results provide support for both evolutionary hypotheses proposed, we are not able to determine the relative strength and validity of these hypothesis. Our rhesus macaques meet the positive condition for both hypotheses: they are terrestrial primates, perform object manipulations, and show mental rotation. Thus, studies with rhesus macaques cannot selectively rule out one hypothesis or the other. In order to make a distinction between these two hypotheses, it is necessary to continue and expand mental rotation research in animals. A range of species must be analyzed, allowing comparisons of those who are terrestrial vs. arboreal and those who show a range of object manipulations vs. those who do not. An ideal species would be the New Caledonian Crow: a clearly arboreal avian species who has been shown to perform purposeful object manipulation for tool use (Weir et al., 2002). If the New Caledonian Crow showed evidence of mental rotation, this would provide exclusive support for the motor planning hypothesis. Within the range of non-human primates, comparison between cebus and spider monkeys, who are both arboreal species but who have been shown to largely vary in their extent of object manipulations, would be fruitful (Torijoe, 1985). Such investigations may help piece apart whether mental rotation is critically linked to ecological demands and perceptual processing, object manipulation and motor planning, or some combination of the two.

It will also be critical for future animal work to test as many subjects as possible. Previous investigations with animals, particularly with non-human primates, is very limited. Most studies have tested only one or two monkeys and each species has been studied no more than a few times. The human work has shown that participants have large individual difference in rotation rate and even strategy (Bethell-Fox & Shepard, 1988; Cooper & Shepard, 1973;

Pylyshyn, 1979). These differences may be related to population variation in general spatial abilities, as it has been found that individuals with low spatial abilities perform more poorly in mental rotation (Shepard & Cooper, 1986). This variation in spatial ability and mental rotation may also be true for animals. In order to truly understand the extent and range of mental rotation ability in nonhuman animals, the field must try to test a greater number of subjects per study and conduct multiple investigations for each species. This will allow stronger comparisons of visual information processing across species and is crucial before valid comparisons can be made between human and nonhuman animals.

Further testing with rhesus macaques and other non-human primates should also evaluate the effects of different procedures and stimuli on monkeys' mental rotation. Differences in attributes of the shapes used, such as complexity, dimensionality, and internal symmetry, may affect the mental rotation rate of humans (Pylyshyn, 1979; Shepard & Cooper, 1986). The different procedures employed over the past few decades, such as sequential or simultaneous presentation of stimuli, have also produced variation in results. Reaction time measurements may capture different parts of the discrimination process in these paradigms and mental rotation rate has been noted to be different across these procedures (Cohen & Kubovy, 1993). Specifically, there is evidence that simultaneous presentation produces greater rates of mental rotation than successive paradigms and may encourage piece meal rotation (Shepard & Cooper, 1986). Studies that compare monkey performance with different shapes and multiple procedures will help elucidate the extent of mental rotation in rhesus macaques and other non-human primate species.

In the future, it would also be interesting to use mental rotation paradigms to investigate dissociations and relationships between maintenance and manipulation of working memory. Mental rotation relies on working memory, using spatial working memory in the dorsal stream for the actual transformation and object working memory in the ventral stream for storage of the intermediate representation (Hyun & Luck, 2007). In rhesus macaques, the majority of working memory research has focused on actively maintaining information in mind across a delay (Miller et. al, 1996). Mental rotation holds promise to study manipulation of working memory in macaques, as it has been argued that mental rotation may be one of the best paradigms to isolate manipulation of working memory performance (Thakkar & Park, 2010). It is possible to give mental rotation tasks without delays as a pure manipulation measure, without rotation as a pure maintenance measure, and with rotation and delays as a joint condition. This type of task would make it possible to investigate dissociations of maintenance and manipulation in working memory. Similar tasks have been used to study differential deficits with a number of patient populations, such as schizophrenic patients (Thakkar & Park, 2010). It would be informative to investigate these same dissociations in non-human primates.

In conclusion, our experiment provides evidence that rhesus macaques perform mental rotation of images in mind to solve mirror image discrimination tasks. These findings provide support for key evolutionary hypotheses about mental rotation, but investigation of mental rotation in a wider range of species is necessary to clarify the evolutionary picture. The fact that these monkeys are capable of this complex spatial transformation calls for increased investigation into mental rotation in non-human primates. In the future, it may be possible to use mental rotation tasks to investigate the spectrum of spatial abilities in non-human primates, to better understand the evolution of visual processing systems across species, to dissociate components of working memory, or even to create animal models for the specific cognitive deficits seen in patient populations.

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Figures

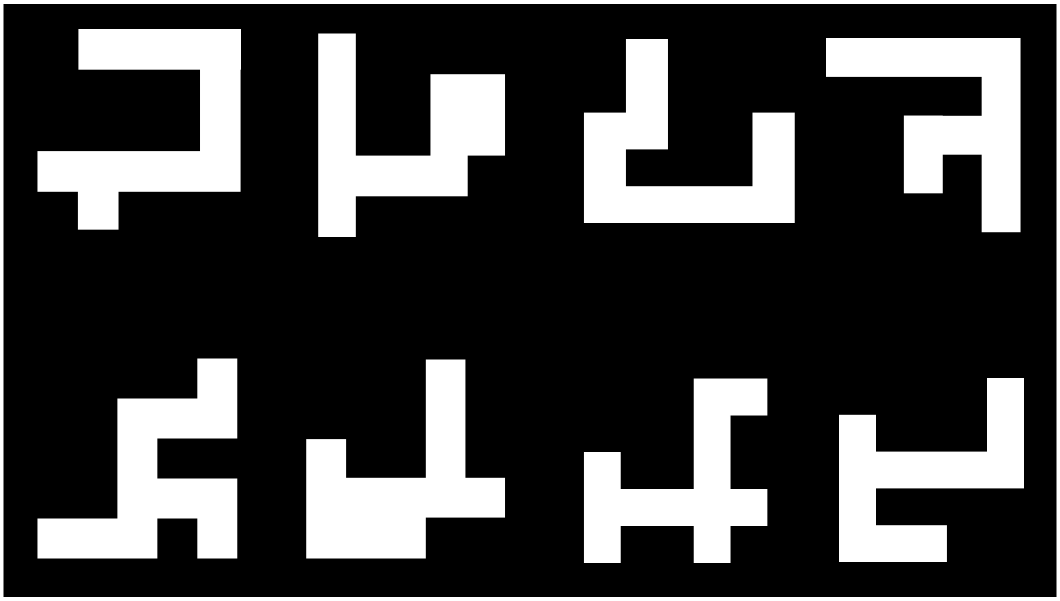

Figure 1. Eight of the sixteen abstract, asymmetrical shapes used as stimuli in the Experiment 1.

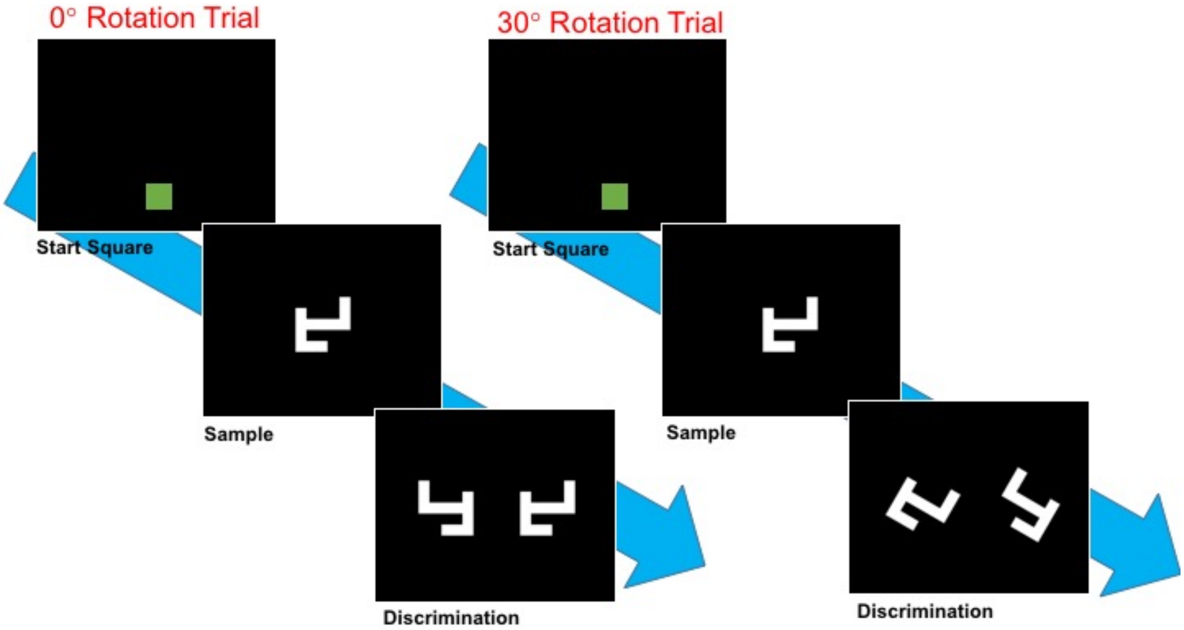

Figure 2. The procedural steps involved in non-rotation *(left)* and rotation *(right)* trials. Trials began when the monkey touched a start square twice. Sample shapes were always presented at the upright orientation. A brief 500-millisecond delay followed sample presentation. Comparison stimuli always included the sample and its mirror image, and these could appear at rotations of 0°, 30°, 60°, 90°, or 120° in the clockwise or counterclockwise direction. Monkeys had to discriminate which of these two images was the previously presented sample.

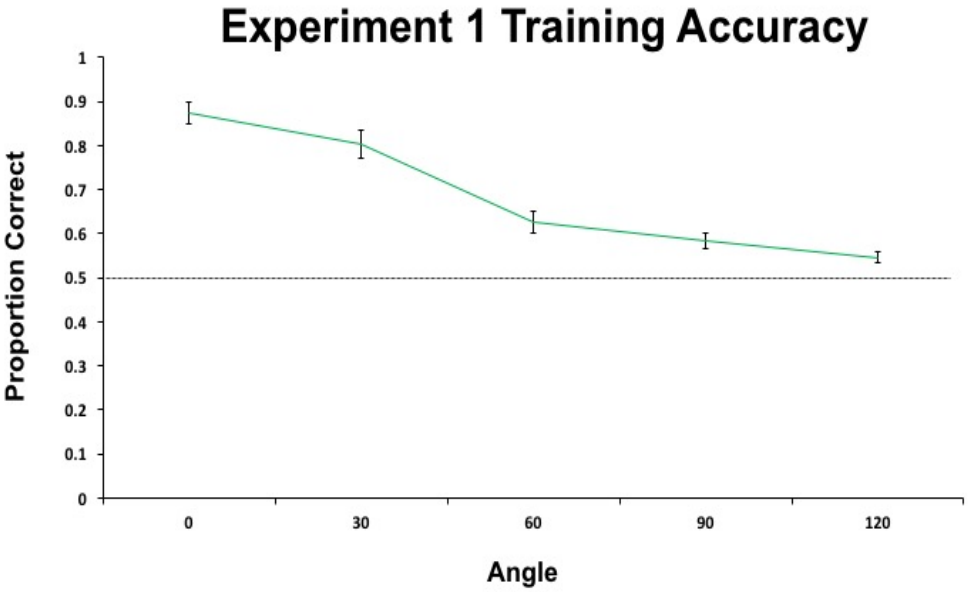

Figure 3. Mean accuracy for the five monkeys for the final twenty sessions of training in Experiment 1. Accuracy is plotted against the angle of comparison stimuli presentation. Error bars are standard error. The small grey dotted line depicts chance performance.

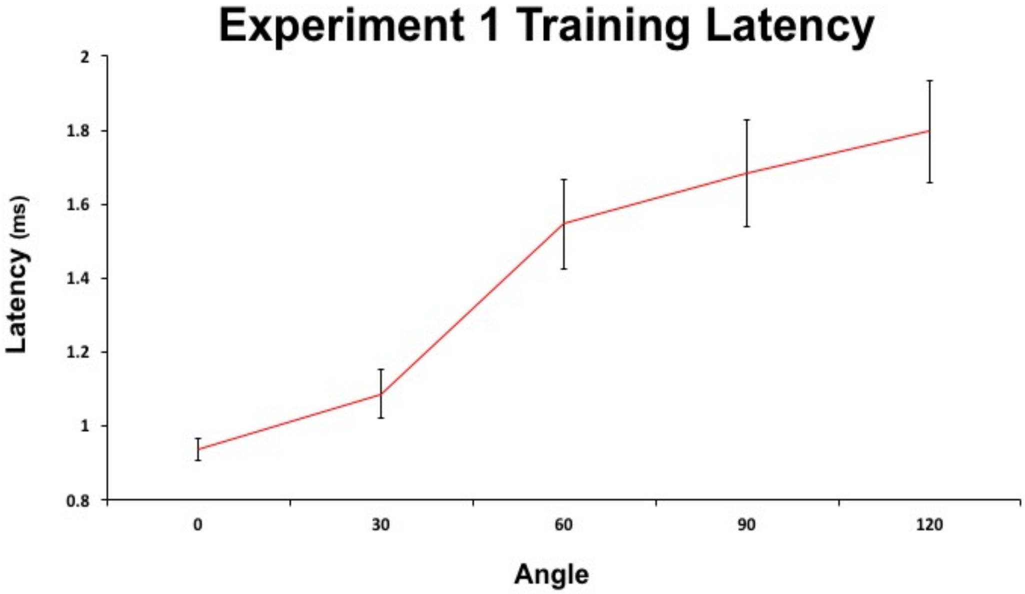

Figure 4. Mean latency for the five monkeys during the final twenty sessions of training in Experiment 2. Reaction time is plotted against angle of rotation of the comparison stimuli. Error bars are standard error.

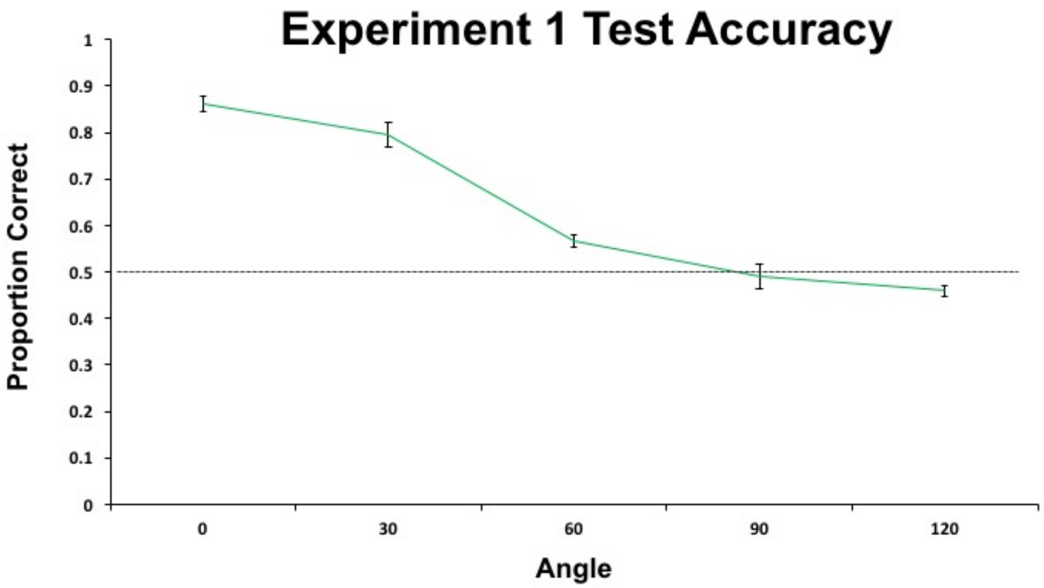

Figure 5. Mean accuracy for the five monkeys during the twenty test sessions of Experiment 1. Accuracy is plotted against the rotation angle of the comparison stimuli. Error bars are standard error.

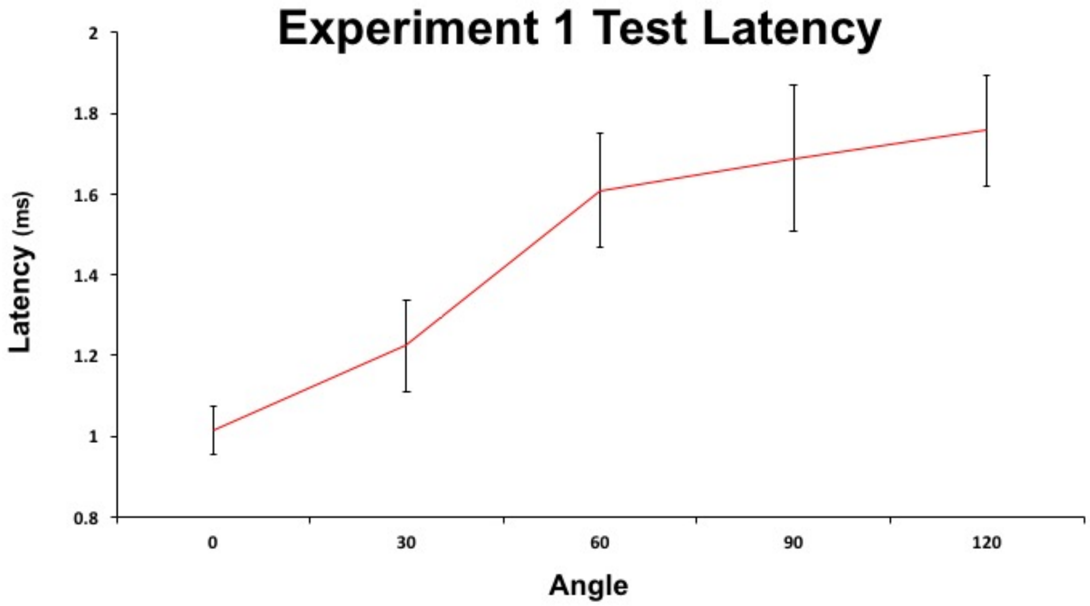

Figure 6. Mean latency for the five monkeys during the twenty test sessions of Experiment 1. Reaction time is plotted against the rotation angle of the comparison stimuli. Error bars are standard error.

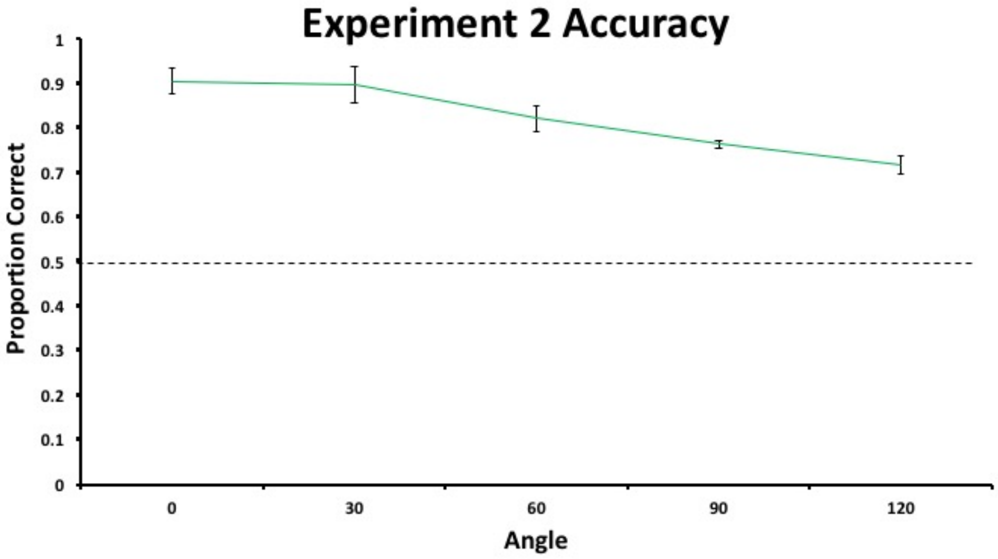

Figure 7. Mean accuracy for the four monkeys during the ten test sessions analyzed for Experiment 2. Proportion correct is plotted against the rotation angle of the comparison stimuli Error bars are standard error.

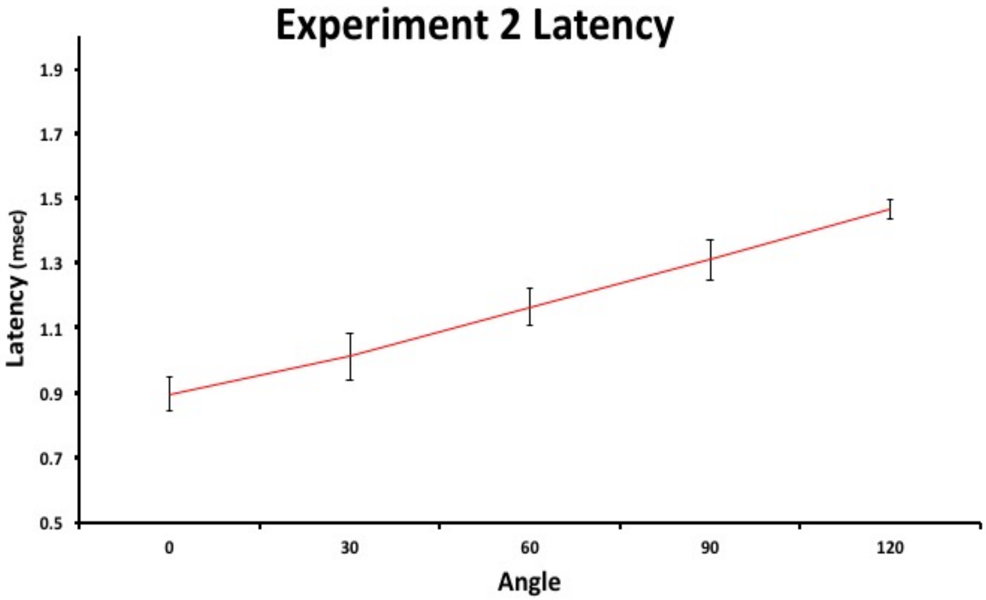

Figure 8. Mean latency for the four monkeys during the ten test sessions analyzed of Experiment 2. Reaction time is plotted against the rotation angle of the comparison stimuli. Error bars are standard error.