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Mental Rotation and Rotational Invariance in the Rhesus Monkey *(Macaca mulatta)*

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Key Words
Mental rotation · Mental representation · Visual information processing · Cognitive ecology · Comparative cognition · Primates · Mammals

Abstract

The mode of visual information processing during visuospatial tasks differs across species and is supposed to depend on evolutionary and ecological factors. Humans show reaction times that increase with angular disparity when tested in mental rotation tasks. Pigeons show a time-independent rotational invariance that possibly evolved in response to the horizontal reference plane birds perceive while flying. As it was suggested that hominids may have secondarily lost the ability of rotational invariance while retreating from arboreal living and evolving upright gait where the vertical reference plane is more important, mental rotation tests with various recent primate species promise to model the evolution of the respective modes of information processing. The results of recent corresponding experiments with a mainly arboreal living primate species could not be explained by either mode, thus supporting the idea of information processing systems having gradually evolved. Here, we conducted mental rotation experiments with three Rhesus monkeys, a more terrestrial living primate species. In a two-alternative matching-to-sample procedure, we measured the monkeys' reaction times for decisions between rotated figures representing image and mirror-image of a previously shown upright sample. The results of our three monkeys were inconsistent. Linear regression analyses showed for one test animal significant correlation coefficients for mean reaction times depending on angular disparity and thus clearly indicated mental rotation. The other two test animals showed reaction times not consistent with mental rotation, whereas rotational invariance might explain the responses to the smaller angles of rotation. Our results suggest that two separately evolved information processing systems may be coexisting to a certain extent in species with correspondingly overlapping ecological demands.

Introduction

The adaptation of animals to different environments has certainly not only strongly influenced their perception of environmental information [Dusenberry, 1992] but also the way in which information is encoded and mentally represented to become usable in cognitive processes. Testing of a special cognitive skill using a given experimental paradigm in various animal species might therefore reveal different information representation and processing systems which could allow animals living in dif-

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ferent environments to process relevant information in the most efficient way. This is exactly what became apparent over the last decades when mental rotation tests were performed with various animal species.

Originally introduced in a classic psychological study by Shepard and Metzler [1971], the mental rotation paradigm was devised as an experimental tool for determining the nature and structure of mental representations used by humans at least during the testing of certain cognitive skills [Shepard and Cooper, 1982]. Shepard and Metzler [1971] found that the time it takes humans to discriminate between the image and mirror-image of rotated figures is linearly dependent on the angular disparity between these figures. This dependency was ascribed to a possibly underlying time-consuming, analogue transformation process of visual information called 'mental rotation' during which the subjects were assumed to rotate an image-like mental representation of the test stimuli.

However, testing pigeons in a mental rotation task Hollard and Delius [1982] found that these birds, unlike humans, are able to discriminate between image and mirror-image of rotated stimuli without delay irrespective of their angular disparity in a time-independent rotational invariance process.

It seems appropriate at this point to introduce the rationale behind the debate for ecological constraints influencing the evolution of visual information processing systems. Besides the more recent argument that mental rotation could even be considered as an imagined (covert) action or is at least partly produced in conjunction with the motor system [Wexler et al., 1998; Wohlschläger, 2001] by having evolved due to the selective advantage of free hands and tool use, there is another argument that is based on aspects of perception, namely vision. The idea was that the ability of humans to generate imagined motion in a cognitive task might stem from the everyday visual perception of the likewise time-consuming physical rotation of real objects [Shepard and Cooper, 1982] and that the same neural substrate might be involved in both processes [Corballis and McLaren, 1982; Jolicoeur and Cavanagh, 1992]. Originally only meant to explain the time-consuming character of the mental rotation process, this argument had further implications by producing testable hypotheses. Hollard and Delius [1982] and Delius and Hollard [1995] argued that the pigeons' rotational invariance could be indicative of an alternative information processing system evolved in response to some special ecological demands of bird vision. During the birds' flight the ground serves as a horizontal reference plane. Therefore, it might be advantageous to birds to recognize the landscape in any orientation without delay. In a study with a California sea lion Mauck and Dehnhardt [1997] reasoned that, similar to birds, species in an aquatic environment could also use horizontal reference planes. For example, marine mammals are assumed to use the bright water surface for orientation while diving and as background to the contrasting dark silhouettes of prey while hunting [Hobson, 1966]. The results of our first experiments [Mauck and Dehnhardt, 1997] did not seem to support this hypothesis as our California sea lion used mental rotation during the same tasks that revealed a time-independent rotational invariance in pigeons [Hollard and Delius, 1982]. However, a follow-up study with this sea lion found that mental rotation of three-dimensional stimuli about the various axes in space differed from that of humans with respect to the priority of axes concerning mental rotation speed [Stich et al., 2003]. Obviously, the special demands of the marine environment encountered by these marine mammals during only a comparatively short period of time in evolution did not trigger a completely different visual information processing system as it has been proposed for pigeons [Hollard and Delius, 1982], but nevertheless changed some interesting details in mental transformation processes as compared to humans. Thus, visual information processing systems in fact seem to be plastic even over evolutionary short periods of time and might be subject to slight changes contingent on the respective environmental demands.

For humans, Delius and Hollard [1995] argued that in the course of evolution – abandoning the arboreal environment and evolving upright gait – hominids might have secondarily lost the ability to efficiently recognize visual stimuli regardless of relative orientations. This hypothesis would be supported if different modes of visual information processing could be traced over a group of recent animal species serving as a model for the corresponding evolutionary steps. Recent primate species with their wide adaptive radiation should provide an interesting group of subjects for this kind of comparative approach. As a first step in this approach we recently tested a lion-tailed macaque, a primate species considered to occupy mainly an arboreal environment, in a mental rotation task [Burman et al., 2005]. The results of the test in this primate species were found to be inconsistent with the mental rotation concept, but also could not be explained by assuming a mere rotational invariance. Thus the data seemed to support the idea of information processing systems having evolved gradually in response to specific ecological demands. In the present study we tested a more

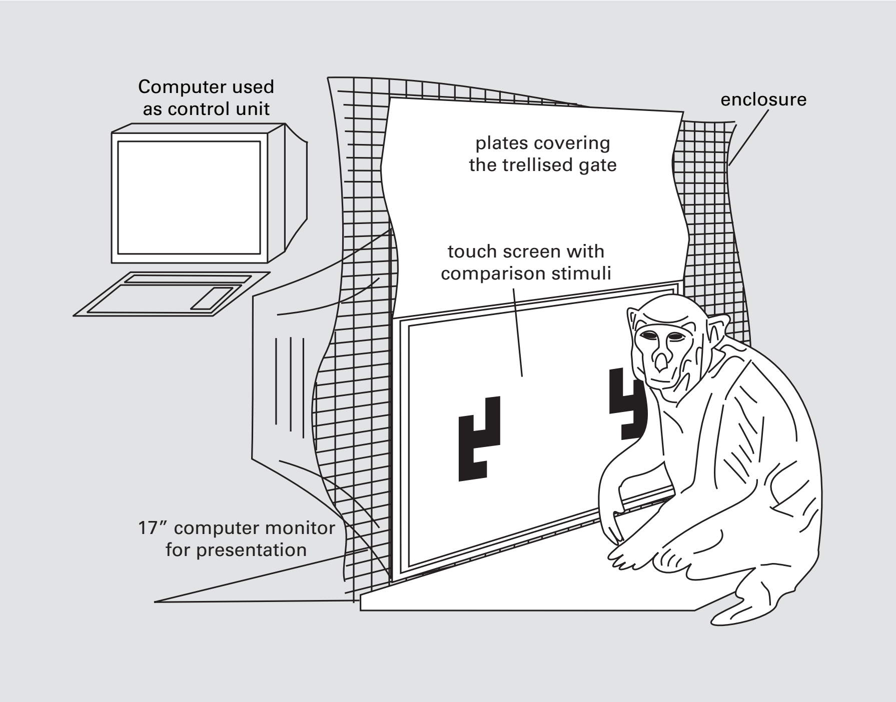

Fig. 1. Schematic drawing of the experimental apparatus.

terrestrial primate species, the Rhesus monkey, using the same experimental paradigm. According to our hypothesis these animals could be expected to show a mode of visual information processing more adapted to the terrestrial environment, and therefore possibly resulting in mental rotation with a human-like reaction time function.

Materials and Methods

Subjects

The study was conducted at the animal housing facility of the University of Bochum, Germany, using three juvenile, experimentally naive Rhesus monkeys *(Macaca mulatta)* named Tom, Paul and Willi. Experiments were conducted in the animals' indoor housing unit. During experimental sessions the respective test animal had to be separated from the group, therefore the experiments were conducted in one of the feeding cages. Experiments were performed in the morning and early afternoon. A typical session consisted of 30 trials, after each session the animal had free access to water. Up to four sessions were performed in direct succession. After the session there was a break of at least one hour with free access to the main cage. A maximum of eight sessions per day were performed with each individual. The animals were not food deprived but received the main part of their food after the experiments. The monkeys were treated in accord with the official German regulations for research on animals.

Stimuli and Test Apparatus

Similar to the recent study by Burman et al. [2005], the stimuli used in the present study were designed for ease of comparison with the results obtained in previous animal studies on mental rotation [Hollard and Delius, 1982; Mauck and Dehnhardt, 1997; Stich et al., 2003]. Each test stimulus was an asymmetric geometrical shape consisting of nine contiguous black squares (1.4 × 1.4 cm). An area of 7 × 7 cm was not exceeded. These geometrical shapes and their mirror-images were rotated by various multiples of 40° and were displayed on an otherwise white computer screen. As in the study by Mauck and Dehnhardt [1997] and by Burman et al. [2005], but in contrast to the study of Hollard and Delius [1982], stimuli were rotated both clockwise and counter-clockwise with respect to the previously shown upright sample. However, rotation angles of clockwise and counter-clockwise rotations were considered equal and were therefore analyzed as rotation angles up to 180°.

A computer-controlled experimental apparatus was used consisting of a standard 17-inch computer screen for stimulus presentation and a touch-screen device was attached in front of the monitor to allow the test animal to react directly to the stimuli. The apparatus was installed in a window in the upper part of the trellised gate of the feeding cage (fig. 1). Sitting on a board in front of the gate the animal could easily touch the apparatus with its hands. The remaining parts of the trellised gate were covered by gray PVC boards in order to exclude any unintentional cueing by the experimenter. A food dispenser was installed above the touch screen next to the apparatus. Both the test apparatus and the food dispenser were connected to a control unit (a standard PC with custom interfaces and custom software programmed in C), which controlled the stimulus presentation, informed the experimenter about the ani-

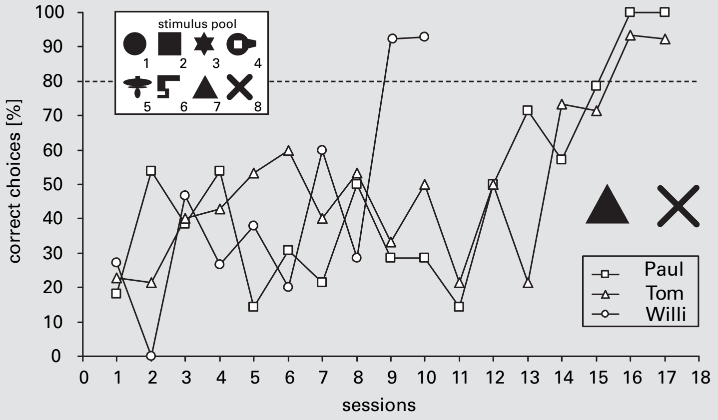

Fig. 2. Exemplary learning curve for acquisition of the matching rule with two stimuli (triangle vs. cross). The inset shows the pool of stimuli used in this phase of the study.

mal's response (correct choice or error) and reaction time and started the food dispenser after correct choices. Reaction time could be measured with an accuracy of 0.005 s.

Experimental Procedure

A successive two-alternative matching-to-sample procedure was used for testing. At the beginning of a session the animal sat down in front of the apparatus following a command by the experimenter. The experimenter started a trial at the control unit computer which switched on the sample in the middle of the touch screen. The animal had to touch the sample within 3 s of presentation time. If the animal failed to do so the trial was aborted and excluded from analysis. After 3 s the sample disappeared and the two comparison stimuli appeared without delay. One comparison stimulus represented the image of the previously shown sample whereas the other was its mirror-image. Both comparison stimuli were shown either in the normal upright orientation or were rotated clockwise or counter-clockwise by the same multiple of 40° [i.e., (±)40, (±)80, (±)120 or (±)160°, respectively]. The appearance of the two comparison stimuli was the signal for the animal to make its choice and at the same time the computer started to measure reaction time. The animal was rewarded for responding to the image of the sample by touching the correct comparison stimulus with its hand. The control computer switched off both comparison stimuli, thus correction of mistakes was impossible. The animal's reaction time was recorded by the computer; correct choices were indicated by an acoustic signal (1 kHz, 0.5 s) and were rewarded through the food dispenser by a peanut, raisin or popcorn. An inter-trial interval of 5 s allowed the monkey to eat the reward and to position itself again in front of the apparatus. There was no punishment for incorrect choices, but a random time-out of 3–8 s was given for incorrect choices in addition to the normal inter-trial interval.

A session consisted of 30 trials, the presentation of comparison stimuli at both positions of the apparatus and the sequence of test stimuli was determined according to pseudorandom schedules [Gellerman, 1933]. The learning criterion was defined as the animal's performance of at least 80% correct choices in at least two successive sessions. However, more sessions were sometimes conducted after the animal reached the criterion in order to establish the animal's performance during acquisition.

Results

As all animals were experimentally naive, the matching procedure as well as image/mirror-image discriminations had to be learned before tests with rotated figures could be performed.

Acquisition of Matching and Image/Mirror-Image Discriminations

Animals were trained to the matching procedure using a pool of 8 stimuli that were thought to present minor difficulties in discrimination (fig. 2, inset). From this pool, stimuli were presented in various pair combinations against each other for a maximum of 30 training sessions with each monkey. For successful completion of this preparation phase of the study, each monkey had to reach the learning criterion (a minimum of 80% correct choices in two successive sessions) with at least one pair of stimuli when these stimuli were presented by themselves in a series of sessions. All monkeys reached this completion criterion. Figure 2 shows the results for a stimulus pair (triangle vs. cross) which yielded a performance of clearly higher than 80% correct choices for all three monkeys. Willi reached the learning criterion within 10 sessions, Paul and Tom reached the criterion within 17 sessions,

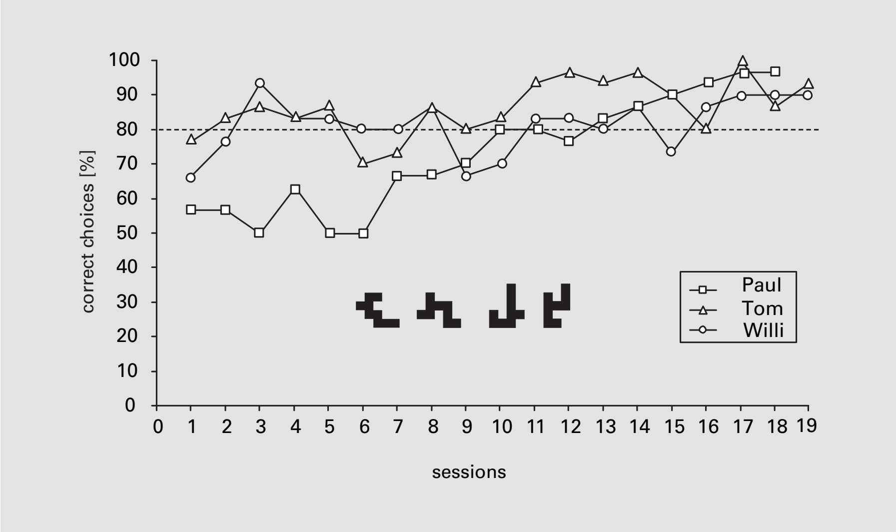

Fig. 3. Performance during acquisition of mirror-image discriminations.

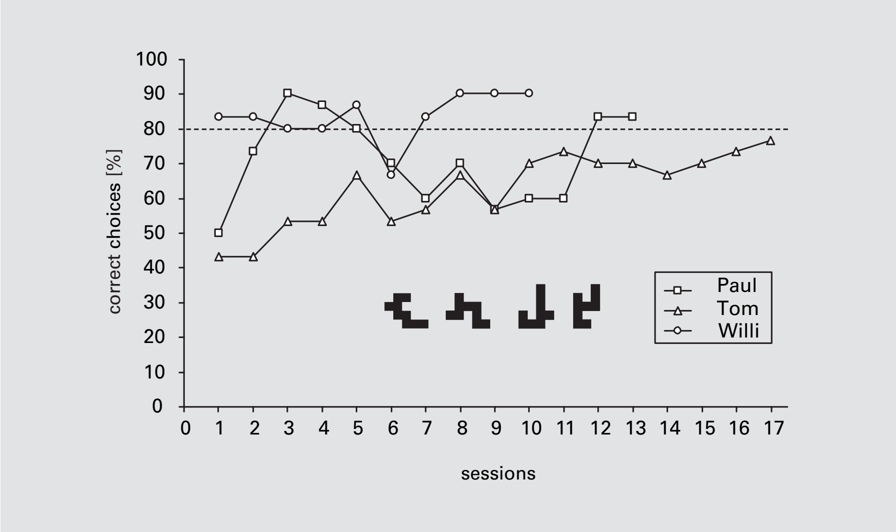

Fig. 4. Performance after introduction of rotated stimuli.

respectively. However, only Tom reached the learning criterion with more than this stimulus pair (i.e., stimulus 3 vs. 5, 6 sessions; stimulus 4 vs. 6, 15 sessions; and stimulus 7 vs. 8, 17 sessions), whereas Paul and Willi showed at least a significant performance level (i.e., at least 70% correct choices, χ^2 test, $\chi^2 \geq 4.8$, $p < 0.05$) only with stimulus 3 vs. 5 (24 and 14 sessions, respectively), but failed to reach both a significant performance level and the learning criterion with further stimulus combinations.

After the monkeys proved that they were able to perform simple matching tasks, the animals were now required for the first time to perform image/mirror-image discriminations. During the next 19 sessions the monkeys were presented with 4 asymmetrical shapes and their mirror-images in their normal upright position (fig. 3). The monkeys were rewarded for choosing the original shape. Tom and Willi surpassed 80% correct choices by the second and third session, respectively, and only fell short of 80% in two and three sessions from then on. Paul reached 80% correct choices only in the 10th session, his performance did not fall short of 80% correct choices after the 13th session. From the 16th session on, the performance of all three monkeys clearly remained over 80% correct choices.

In the final preparation stage of the study the monkeys learned to perform image/mirror-image discriminations with rotated comparison stimuli. The same stimulus pool

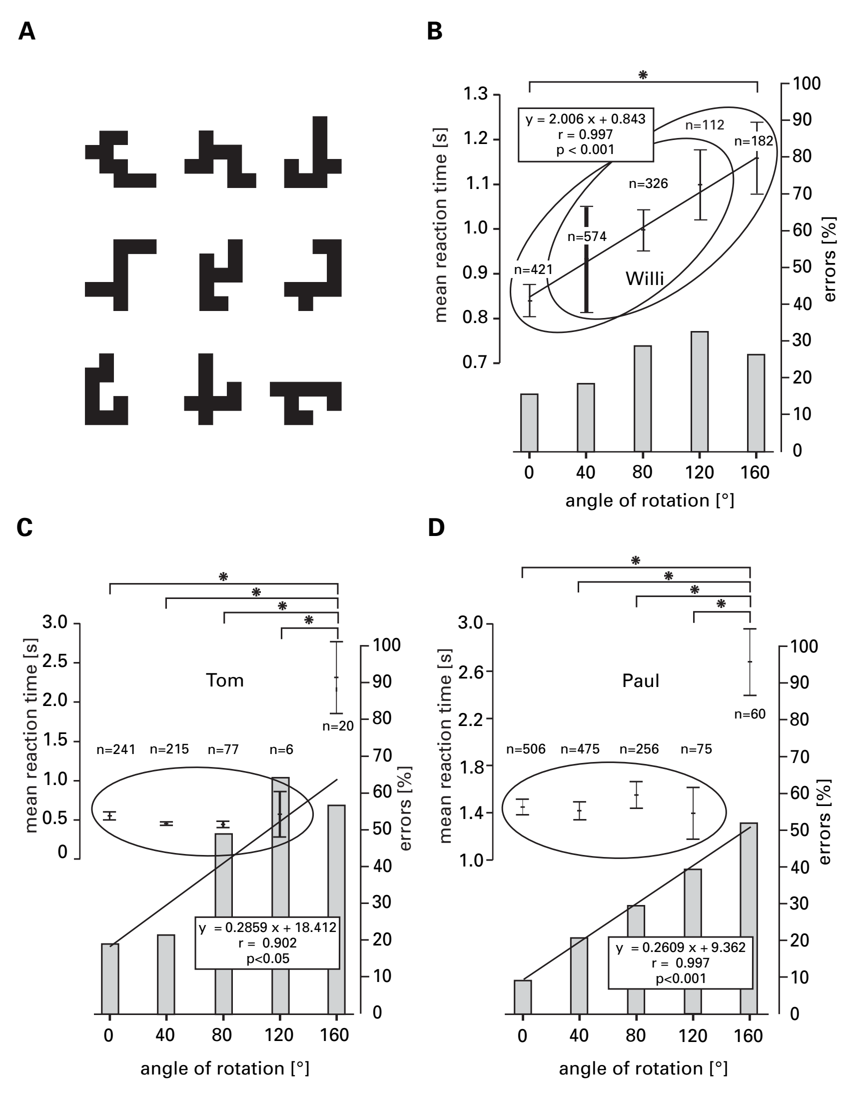

Fig. 5. A Pool of stimuli used in this phase of the study. **B–D** Overall evaluation of the respective monkey's performance (grey bars) and mean reaction times (ticks with SD) as a function of the angle of rotation. Encircled datapoints denote homogenous subgroups of reaction times as shown by ANOVA and Scheffé post-hoc tests. Note that scaling of the y-axes denoting mean reaction times differ in parts **B–D**. * Significant difference between reaction times as shown by ANOVA and Scheffé post-hoc tests.

as in the previous stage was used, but both comparison stimuli were rotated by 40, 80 or sometimes even 120°. Although the performance of Tom was strongly impaired by the introduction of rotation trials and only reached the level of significance in the 10th session, Paul's performance surpassed 80% correct choices by the third session and Willi's performance was not at all impaired (more than 80% correct choices from the first session on). To achieve a stable performance in this preparation phase, training with Willi and Paul was extended to the 10th and 13th session, respectively. The training with Tom, however, was terminated after the 17th session when he had reached a clearly significant level of performance (i.e., at least two consecutive sessions with 70% correct choices, χ^2 test, $\chi^2 \geq 4.8$, $p < 0.05$). This performance was considered a sufficient basis for starting the measurements of reaction times.

Measurement of Reaction Times

A total of 154 sessions was evaluated for the three tested monkeys. Each session consisted of 30 trials, and was composed of both rotation and non-rotation trials. A pool of 9 asymmetrical stimuli was used (fig. 5A). Comparison stimuli in rotation trials were rotated by 40, 60, 120 and 160° clockwise and counterclockwise, respectively. Rotation of comparison stimuli in both possible directions, the presentation of comparison stimuli at both positions of the touch screen and the sequence of test stimuli during a session were arranged according to pseudorandom schedules [Gellerman, 1933].

For each monkey only those sessions during which the respective test animal reached a performance significantly different from chance were included in the analysis (i.e., at least 70% correct choices, χ^2 test, $\chi^2 \geq 4.8$, $p < 0.05$). This way, for the three monkeys 26 (Tom), 59 (Paul) and 69 (Willi) sessions with a total of 780 (Tom), 1,770 (Paul) and 2,070 (Willi) trials could be included in the analysis.

From these sessions, the animals' accuracy of choice and mean reaction times from correct choices during both rotation trials and non-rotation trials were calculated for every absolute angle of rotation. One-way-ANOVAs showed significant differences between the respective reaction times of the three monkeys for non-rotation trials and for the four absolute angles of rotation (i.e., 0°: F(2, 1,165) = 234.974, $p < 0.001$; 40°: F(2, 1,261) = 59.96, $p < 0.001$; 80°: F(2, 658) = 107.426, $p < 0.001$; 120°: F(2, 190) = 6.919, $p < 0.01$; 160°: F(2, 259) = 104.158, $p < 0.001$), only one homogenous subgroup was found by a Scheffé post-hoc test (160° rotation trials for Paul and Tom). It was therefore decided not to pool the data for the three monkeys but to analyze reaction times and error rates separately.

Mean reaction times with standard deviations and percentage of errors was plotted for each monkey against the absolute angle of rotation (fig. 5 B–D). Generally there was a tendency for error rates to be higher for rotation trials than for non-rotation trials and to increase with angular disparity; linear regression analyses yielded significant correlation coefficients for Tom ($r = 0.902$, $p < 0.05$) and Paul ($r = 0.997$, $p < 0.001$; fig. 5C, D). Error rates increased with angular disparity for Willi as well (fig.5B), but this linear correlation was not significant ($r = 0.789$, $p > 0.05$). One-way ANOVAs with Scheffé post-hoc tests found significant differences between reaction times for the tested angles of rotation for all three monkeys [Willi: F(4, 1,610) = 4.666, $p < 0.001$, two homogeneous subgroups: 0, 40, 80 and 120° ($p = 0.065$) and 40, 80, 120 and 160° ($p = 0.146$), Tom: F(4, 554) = 128.036, $p < 0.001$, one homogeneous subgroup: 0, 40, 80 and 120° ($p = 0.853$); Paul: F(4, 1,367) = 30.86, $p < 0.001$, one homogeneous subgroup: 0, 40, 80 and 120° ($p = 0.695$)]. Only for one of the monkeys (Willi) did a linear regression analysis for all absolute angles of rotation yield a significant correlation coefficient for reaction times ($y = 2.006x + 0.843$, $r = 0.997$, $p < 0.001$) as correlated with angular disparity. Two further linear regression analyses conducted separately for both homogenous subgroups also yielded significant correlation coefficients for Willi (i.e., 0–120°, $y = 2.102x + 0.839$, $r = 0.997$, $p < 0.01$ and 40–160°, $y = 1.953x + 0.85$, $r = 0.995$, $p < 0.01$, respectively).

Discussion

The present experiments were performed as part of a comparative approach using a mental rotation paradigm with different recent primate species to test the idea that visual information processing systems might have evolved in response to ecological demands of the animals' respective environments. Similar to the test animals used in previous studies [Mauck and Dehnhardt, 1997; Stich et al., 2003 Burman et al., 2005], the Rhesus monkeys used in the present study had to fulfill some basic experimental requirements.

As a first requirement, the monkeys had to master the matching-to-sample procedure. Although the monkeys seemed to have some difficulties with this task and a good performance could not be established for all stimuli, all monkeys fulfilled the criterion of reaching 80% correct choices in two successive sessions with at least one pair of stimuli. During sessions with some of the remaining stimuli resulting in non-significant performance, the monkeys might have been not only affected by the so-called 'novelty effect' that often causes neophobic responses after introducing new stimuli during matching-to-sample tasks [D'Amato et al., 1985], but their performance might also have been impaired by a generally aversive effect of some of the stimuli. However, we did not intend to conclude from these results that the monkeys applied a concept-like matching rule [this would require a sufficiently large sample size of first-trial data; Oden et al., 1988; Thomas and Noble, 1988; Schusterman and Kastak, 1993], because this does not seem to be necessary during mental rotation tasks [compare Mauck and Dehnhardt, 1997; Stich et al., 2003; Burman et al., 2005]. Therefore, the monkeys' performance in this preparation stage was considered to be sufficient to enter the next training phase.

The mental rotation concept can only be tested in the classical way if the subjects are able to reliably perform image/mirror-image discriminations, which cannot be taken for granted in animals [for a review see Corballis and Beale, 1976]. Pigeons have much more difficulty in discriminating mirror-image patterns than discriminating arbitrarily different pairs of patterns [Lohmann et al., 1988]. They find mirror-image patterns especially difficult to discriminate if the patterns are reflected along their vertical axis [Todrin and Blough, 1983]. However, Delius and Hollard [1995] found evidence that pigeons – at least in comparison with humans – have less difficulty with mirror-images than with arbitrary shapes. The sea lion tested in two of our previous studies on mental rotation likewise learned mirror-image discriminations with little difficulty, even with three-dimensional stimuli [Mauck and Dehnhardt, 1997; Stich et al., 2003]. A previous study found that Rhesus monkeys have some difficulties with mirror-images [Brown and Ettlinger, 1983; compare also Nissen and McCulloch, 1937 for chimpanzees and Sanford and Ward, 1986 for bushbabies]. Although our monkeys seemed to have some difficulties during acquisition of the basic matching procedure, they obviously had little difficulty applying the matching rule to the discrimination of mirror-images with asymmetrical patterns. The initial performance of two of our monkeys in the mirror-image discrimination task (fig. 3) compares well with that of the lion tailed macaque recently tested [Burman et al., 2005], which likewise transferred the matching procedure to the mirror-images immediately and without difficulty. Our third Rhesus monkey had to learn the mirror-image discrimination, but succeeded in doing so within a few sessions and was therefore considered sufficiently trained for the next preparation stage.

Similar to the introduction of mirror-image discriminations, the introduction of rotated stimuli seemed to be a problem for only one of our Rhesus monkeys (fig. 4). However, because the stimuli used in this preparation stage were to be partly used in the testing stage as well, training was terminated as soon as this monkey had reached a level of performance significantly different from chance (after 17 sessions). However, with a comparable learning effort as the sea lion in the study of Mauck and Dehnhardt [1997] and the lion-tailed macaque tested by Burman et al. [2005], all three monkeys were also able to apply the matching rule to rotated figures when this final preparation phase was terminated and the measurement of reaction times began.

Interestingly, the analysis of mean reaction times and error rates yielded inconsistent results for our three monkeys. One of the monkeys showed reaction times clearly increasing with the angle of rotation and corresponding linear regression analysis yielded a highly significant correlation coefficient (fig. 5B). Although reaction times as correlated with angular disparity can be subdivided into two homogeneous subgroups (i.e., 0–120° and 40–160°), there seems to be no obvious discrepancy between these two subgroups concerning the slope of reaction time (0–120°, $m = 2.102$ and 40–160°, $m = 1.953$, respectively, see also fig. 5B). The general tendency for error rates to be higher for rotation trials than for non-rotation trials and to increase with angular disparity was found for this animal as well, although a linear regression analysis yielded a high but non-significant correlation coefficient ($r = 0.789$, $p > 0.05$). Thus, the overall results certainly fulfill the criteria to assume that this monkey solved the task using a mental rotation strategy.

Most interestingly, the first homogeneous subgroup concerning reaction times (0–120°) was also found in the other two monkeys (fig. 5C, D), which did not yield significant correlation coefficients in linear regression analyses of reaction times and thus would not be assumed to have used a mental rotation strategy. Obviously, mean reaction times for non-rotation trials and for the smaller angles of rotation (40–120°) do not increase with angle of rotation (i.e., there were no significant differences between reaction times for 0, 40, 80 and 120° and there is no obvious increase in reaction time with angular disparity). However, this homogenous subgroup differed significantly from mean reaction time for 160°, which is clearly higher for both monkeys.

Although error rates with angles of rotation show a linear increase for these two monkeys, the results for the reaction times lead us to assume that they might have applied two separate response strategies depending on the angle of rotation. The responses of both monkeys to the smaller angles of rotation (0–120°) could be explained by a kind of rotational invariance (mean reaction times do not increase with angle of rotation) whereas this model cannot explain the high response latencies found for the highest angle of rotation (i.e., 160°; fig. 5C, D). Obviously, the rotational invariance strategy failed to succeed for this high degree of angular disparity.

However, the finding of more than one information processing model used by primates is not completely new. For example, Vauclair et al. [1993] showed that baboons display a human-like mental rotation effect when discriminating mirror-image shapes they see in their right optical hemifield, but a pigeon-like flat invariance function when they see the shapes in their left optical hemifield. These results have been interpreted to show, at least in principle, that the mammalian, specifically the primate geniculocortical system, is just as suited for parallel processing of mirror-image orientation invariance as the avian tectoectostriatal system [Delius and Hollard, 1995]. Recently, we suggested the evolution of a visual information processing system in lion-tailed macaques some-where in between mental rotation and rotational invariance [higher reaction times for rotation than for non-rotation trials but non-increasing reaction times for all tested angles of rotation; Burman et al., 2005]. The present finding of a kind of rotational invariance applied only to the smaller angles of rotation thus seems to confirm the idea of gradually modified information processing systems. The question by which mode of information processing our monkeys solved the task with the highest angle of rotation (i.e., 160°) remains unanswered. However, it is obvious that whatever strategy they used for these higher angles of rotation, it clearly seems to work less efficiently than the rotational invariance-like strategy they were able to apply to the smaller angles of rotation (significantly higher reaction times and clearly more errors for 160°) and also less efficiently than the mental rotation strategy (clearly more errors and significantly higher reaction times as shown by ANOVA than found for Willi for 160° trials).

In summary, our results support the idea of two separately evolved information processing systems – mental rotation and rotational invariance – and the evolution of various specially adapted intermediates. Moreover, our results show for the first time that – given correspondingly overlapping ecological demands – two separately evolved information processing systems might coexist to a certain extent in different individuals of the same species.

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