Research Report

ROTATION OF MENTAL IMAGES IN BABOONS WHEN THE VISUAL INPUT IS DIRECTED TO THE LEFT CEREBRAL HEMISPHERE

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Abstract—The mental rotation phenomenon was examined in baboons and humans using a video-formatted matching-to-sample task. Sample stimuli were presented either centrally or in the right or left visual half-field. Immediately afterward, subjects had to distinguish the previously presented sample stimulus from its mirror image after both had been rotated to the same angular deviation. A mental rotation phenomenon was found in baboons and humans, but in baboons this effect was limited to conditions in which visual input was directed to the right visual half-field. These data represent the first evidence of mental rotation in a nonhuman species.

A great deal of evidence suggests that humans are capable of mentally rotating perceived or imagined visual forms (Corballis, 1988, Shepard & Metzler, 1971). The test of mental rotation implies a comparison between a previously presented visual sample stimulus and the display of the same stimulus depicted in different orientations. A typical result in mental rotation tasks is that decision time increases linearly with the angular disparity of the patterns (Cooper & Shepard, 1973, Pylyshyn, 1973, Shepard & Metzler, 1971). This phenomenon has been explained by suggesting that subjects mentally rotate one visual pattern into congruence with the other (Shepard & Metzler, 1971). It has never been demonstrated that a nonhuman species is capable of mentally rotating visual stimuli. One study (Hollard & Delius, 1982) reported that pigeons were able to discriminate shapes despite changes in orientation, but these animals did not show the humanlike relation between decision time and the degree of angular rotation.

The present research shows that baboons are able to mentally rotate internal representations of visual stimuli. The mental rotation process also has been shown to be lateralized in humans (Corballis & Sergent, 1989, Kosslyn, 1987). While there are no studies on hemispheric specialization for mental rotation in any nonhuman species, recent evidence suggests that anatomical and functional population asymmetries may not be unique to humans (Fagot & Vauclair, 1991, Glick, 1985, MacNeilage, Studdert-Kennedy, & Lindblom, 1987). In the current study, we combined recent technological developments in the control of visual fixation for unilateral presentation of stimuli in nonhuman primates (Hopkins, Washburn, & Rumbaugh, 1990) with the mental rotation paradigm.

METHODS

Six wild-born juvenile baboons (Papio papio), 3 males and 3 females, were trained and tested with the apparatus shown in Figure 1. The method of testing was based on the paradigm of matching to sample using rotated visual stimuli. The testing environment (top of Fig 1) comprised an experimental cage fitted with a viewpoint, two hand ports, and a food dispenser. A touch-sensitive pad, a joystick, and a 14-in color monitor were positioned on the horizontal axis of the cage. The experimental cage was located in a room lighted with a 60-W bulb vertically fixed above the cage.

To initiate a trial, subjects had to place a hand on the touch pad. Trials began with the appearance of a green cursor (0.5 cm in diameter) in the center of the monitor and a fixation stimulus (a 0.6-cm white square) 1.5 cm above or below the cursor. Subjects had to manipulate the joystick to precisely align the cursor within the boundaries of the fixation stimulus for 25 ms. This constraint allowed for control of eye fixation. After fixation, a yellow sample shape was presented laterally for 150 ms (bottom left of Fig 1). According to Fuchs (1967), the latency for saccadic eye movements in monkeys ranges between 200 and 250 ms. Thus, the duration of stimulus presentation (150 ms) was sufficient to prevent saccadic eye movements during sample presentation. Presentation of the sample stimulus was followed immediately by the display of two yellow comparison shapes (bottom right of Fig 1). One comparison stimulus matched the sample stimulus, the other was the left-right mirror image. Moving the cursor, by way of joystick manipulation, to the location of the matching comparison stimulus was food reinforced. Incorrect responses were not reinforced.

Three baboons used the right hand to manipulate the joystick, and the 3 others used the left hand. Prior to the experiment, subjects were trained with the video-formatted apparatus to perform the matching-to-sample task using asymmetric patterns (Hopkins, Fagot, & Vauclair, 1993). The critical feature of our procedure was the capability of presenting stimuli unilaterally and thus to lateralize the visual input in one cerebral hemisphere.

During testing, each baboon received four test sessions of 144 trials each. Test Sessions 1 and 2 corresponded to Block 1. Test Sessions 3 and 4 corresponded to Block 2. The stimuli used in Sessions 1 to 4 were the letters F, P, F, and R, respectively. Within a session, the designated letter and its mirror image were utilized as sample shapes and were always presented in their upright orientation. Trial presentation was constrained by the requirement that the positive
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85.9 (M = 70.4%, SD = 11.2) Chi-square analyses were performed to determine if individual subjects performed significantly (p < 0.05) above chance. Two animals were at chance level, whereas the remaining 4 were significantly above chance. Therefore, data from the 2 less-accurate subjects were omitted from further analyses.

For the remaining 4 baboons, the percentage correct ranged from 72.4 to 85.9 (M = 77.6%, SD = 5.4). To assess overall performance, an analysis of variance (ANOVA) was performed on accuracy data, with block, eccentricity, and orientation serving as independent variables. A significant Orientation x Eccentricity interaction was found, F(10, 30) = 3.00, p < 0.05. This interaction is depicted in Figure 2. It appears from Figure 2 that the interaction is mainly due to the data for 0° eccentricity. A separate Block x Orientation ANOVA at 0° eccentricity revealed a significant orientation effect, F(5, 15) = 7.03, p = 0.001. In the case of 0°, post hoc analyses (Tukey honestly significant difference, HSD, p < 0.05) revealed that the proportion of errors at 180° orientation was significantly greater than at 0°, 60°, and 300°. For 4° eccentricity, a Block x Orientation x Field ANOVA revealed a field effect, F(1, 3) = 15.58, p < 0.05, as the unique significant effect. Accuracy was significantly better in the right visual field (M = 79%) than in the left visual field (M = 75%).

The relatively poor performance of the baboons at 0° eccentricity on trials with the greatest angular disparities supports our earlier contention that lateralized presentation enhances solution of mental rotation problems (Hopkins et al., 1993). Additional support for this conclusion comes from the data indicating no significant relationship between accuracy and angular disparity at eccentricities of 4° and 8° (see Fig. 2).

Only correct trials were considered for analysis of response times. Response times less than 100 ms (n = 13) were discarded from the analysis since they most likely reflected an anticipation response. These trials represented less than 1% of the total number of correct responses. Regarding response times specific to unilateral presentations, an ANOVA with independent variables of block, eccentricity, orientation, and visual half-field revealed a significant ori-

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Fig 1: Apparatus and stimuli. The upper figure illustrates the testing environment, which comprised an experimental cage fitted with a viewport (A), two hand ports (B), a food dispenser (C), a touch-sensitive pad (D), a joystick (E), and a 14-in color monitor (F). The bottom figures illustrate the lateral display of the sample stimuli on the monitor (left) and the presentation of the two comparison mirror-image stimuli (right).

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Comparison stimulus not appear in the same position on more than 3 consecutive trials. Sample stimuli were displayed either centrally (0° eccentricity) or at 4° or 8° of eccentricity relative to the fixation point (Eccentricity is defined as the lateral displacement of the stimulus from the central fixation point). For both humans and monkeys, an eccentricity between 2° and 3° is considered adequate for unilateral presentation as long as the stimuli are presented faster than the time needed for saccadic eye movements (Bryden, 1982; Leventhal, Ault, & Vitek, 1988). Eccentricity was determined by considering the innermost side of the sample stimulus relative to the center of the fixation point. For 4° and 8° eccentricities, sample stimuli were displayed in the left or right visual half-field following a random order. In an equal number of trials per session, the comparison shapes were oriented at 0°, 60°, 120°, 180°, 240°, or 300°.

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RESULTS

The percentages of correct responses for the 6 baboons ranged from 56.0 to 85.9 (M = 70.4%, SD = 11.2). Chi-square analyses were performed to determine if individual subjects performed significantly (p < 0.05) above chance. Two animals were at chance level, whereas the remaining 4 were significantly above chance. Therefore, data from the 2 less-accurate subjects were omitted from further analyses.

For the remaining 4 baboons, the percentage correct ranged from 72.4 to 85.9 (M = 77.6%, SD = 5.4). To assess overall performance, an analysis of variance (ANOVA) was performed on accuracy data, with block, eccentricity, and orientation serving as independent variables. A significant Orientation x Eccentricity interaction was found, F(10, 30) = 3.08, p < 0.01. This interaction is depicted in Figure 2. It appears from Figure 2 that the interaction is mainly due to the data for 0° eccentricity. A separate Block x Orientation ANOVA at 0° eccentricity revealed a significant orientation effect, F(5, 15) = 7.03, p = 0.001. In the case of 0°, post hoc analyses (Tukey honestly significant difference, HSD, p < 0.05) revealed that the proportion of errors at 180° orientation was significantly greater than at 0°, 60°, and 300°. For 4° eccentricity, a Block x Orientation x Field ANOVA revealed a field effect, F(1, 3) = 15.58, p < 0.05, as the unique significant effect. Accuracy was significantly better in the right visual field (M = 79%) than in the left visual field (M = 75%). The relatively poor performance of the baboons at 0° eccentricity on trials with the greatest angular disparities supports our earlier contention that lateralized presentation enhances solution of mental rotation problems (Hopkins et al., 1993). Additional support for this conclusion comes from the data indicating no significant relationship between accuracy and angular disparity at eccentricities of 4° and 8° (see Fig. 2).

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100
Fig 2 Percentage of correct responses for each eccentricity and orientation. Circle = 0° eccentricity, square = 4° eccentricity, triangle = 8° eccentricity.

entation × Visual Half-Field interaction, \(F(5, 15) = 5.53, p < 0.05\) No other main effects or interactions were significant.

Individual mean response times for each visual half-field and orientation, averaged across the 4° and 8° eccentricities, are presented in Table 1. The mean response times, averaged across subjects, as a function of orientation and visual half-field can be seen in Figures 3a and 3b. Trend analyses within each visual half-field were performed to determine whether the relation between orientation and response time could fit an optimal mental rotation curve. The coefficients of contrast corresponding to the optimal curve were -3, -1, 1, 3, 1, and -1 for the 0°, 60°, 120°, 180°, 240°, and 300° orientations, respectively (Sargent & Corballis, 1989). For the right-visual-field (RVF) presentations, 83% of the variance was accounted for by this optimal mental rotation curve, \(F(1, 4) = 19.1, p < 0.02\). For the left-visual-field (LVF) presentations, only 23% of the variance was accounted for by this curve, an amount which failed to reach significance, \(F(1, 4) = 1.24\). Thus, a mental rotation effect was found for RVF presentations, suggesting that the left hemisphere utilized a humanlike mental rotation strategy. Analysis of the data at 0° eccentricity failed to reveal any significant effect.

### Table 1

<table>
<thead>
<tr>
<th>Degree of orientation</th>
<th>Right visual half-field</th>
<th>Left visual half-field</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Subject 1</td>
<td>Subject 2</td>
</tr>
<tr>
<td>0</td>
<td>292</td>
<td>406</td>
</tr>
<tr>
<td>60</td>
<td>313</td>
<td>392</td>
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</tr>
<tr>
<td>300</td>
<td>293</td>
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</tr>
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</table>
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Response time was 207 ms for the humans, but 18 ms for the baboons

DISCUSSION

A prerequisite for mental rotation testing within the matching procedure is the ability to discriminate mirror images, an ability some investigators have claimed is beyond the capacity of non-human species, including primates (Corbally & Beale, 1976). In the present study, we have demonstrated that baboons are capable of mirror-image discriminations despite spatial transformations involving various disorientations (Fig 2). Additionally, contrary to the study with pigeons (Holland & Delius, 1982), baboons were not specifically trained with mirror-image or rotated shapes. Why, then, were the baboons so efficient? We believe that the answer lies in the mode of stimulus presentation. We suggest that unilateral presentations of sample stimuli result in greater resolution of the object representation in the contralateral than the ipsilateral hemisphere. We speculate that this discrepancy in resolution might be due to a loss of information during interhemispheric transfer. This effect, produced by our behavioral procedure or surgical procedures such as transection of the corpus callosum (Noble, 1966), appears to facilitate mirror-image discrimination.

We tested a small sample of human subjects to investigate the efficiency of our method to tap mental rotation in humans. The human data revealed the presence of mental rotation curves for both LVF and RVF presentations. This result is consistent with the literature (e.g., Kosslyn, Berndt, & Doyle, 1985). Typically, although both hemispheres in humans use a mental rotation strategy, one hemisphere is found to be more affected by the disorientation than the other (Corbally & Sergent, 1989). Our sample of human subjects was presumably too limited to reveal such an effect.

For baboons, accuracy for RVF presentations was significantly greater than for LVF presentations at an eccentricity of 4°. This result is consistent with previous reports indicating a left-hemisphere advantage for visual-spatial discrimination in monkeys (Hamilton & Vermeire, 1988, Jason, Cowley, & Weiskrantz, 1984), although it is not entirely consistent with human findings (Sergent & Corbally, 1989). In this respect, the nonhuman primate literature on cognitive lateralization does not always offer a consistent picture with the human literature. Several factors (e.g., species, task demands, stimuli) probably explain the discrepancies, and further study is needed. Nevertheless, the present study demonstrates that the two halves of the baboon brain differentially process visual imagery. This finding provides additional behavioral support for the existence of cognitive lateralization in monkeys.

Explaining the differences in response times as well as mental rotation rates between humans and baboons will require follow-up investigations. At present, any explanation remains speculative. However, the letter stimuli used in this study have a specific meaning or reinforcement history to human subjects that does not exist in baboons. This fact may account for some of the differences in response times. Alternatively, we would not rule out other factors, such as the overall size of the brain, overall dif-
Fig 4 Humans' response times as a function of orientation for shapes presented in the left visual half-field (a) and in the right visual half-field (b)

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