

## 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 viewport, 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 be-

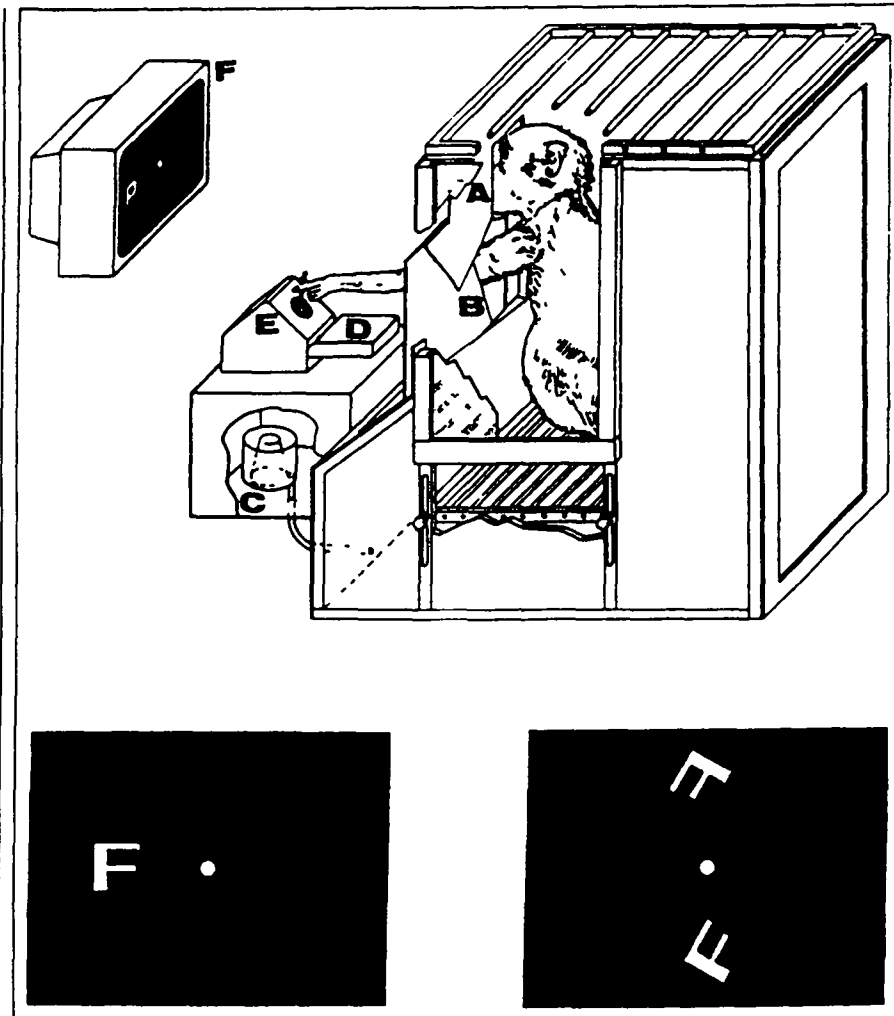
low the cursor. Subjects had to manipulate the joystick to precisely align the cursor within the boundaries of the fixation stimulus for 25 ms. This constraint allowed for control of eye fixation. After fixation, a yellow sample shape was presented laterally for 150 ms (bottom left of Fig. 1). According 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 its 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*, *P*, and *F*, 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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## Mental Rotation in Baboons



**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).

comparison stimulus not appear in the same position on more than 3 consecutive trials. Sample stimuli were displayed either centrally ( $0^\circ$  eccentricity) or at  $4^\circ$  or  $8^\circ$  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  $2^\circ$  and  $3^\circ$  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 deter-

mined by considering the innermost side of the sample stimulus relative to the center of the fixation point. For  $4^\circ$  and  $8^\circ$  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  $0^\circ$ ,  $60^\circ$ ,  $120^\circ$ ,  $180^\circ$ ,  $240^\circ$ , or  $300^\circ$ .

## 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 ( $p < .05$ ) 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  $\times$  Eccentricity interaction was found,  $F(10, 30) = 3.08$ ,  $p < .01$ . This interaction is depicted in Figure 2. It appears from Figure 2 that the interaction is mainly due to the data for  $0^\circ$  eccentricity. A separate Block  $\times$  Orientation ANOVA at  $0^\circ$  eccentricity revealed a significant orientation effect,  $F(5, 15) = 7.03$ ,  $p = .001$ . In the case of  $0^\circ$ , post hoc analyses (Tukey honestly significant difference, HSD,  $p < .05$ ) revealed that the proportion of errors at  $180^\circ$  orientation was significantly greater than at  $0^\circ$ ,  $60^\circ$ , and  $300^\circ$ . For  $4^\circ$  eccentricity, a Block  $\times$  Orientation  $\times$  Field ANOVA revealed a field effect,  $F(1, 3) = 15.58$ ,  $p < .05$ , 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  $0^\circ$  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 relation between accuracy and angular disparity at eccentricities of  $4^\circ$  and  $8^\circ$  (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-

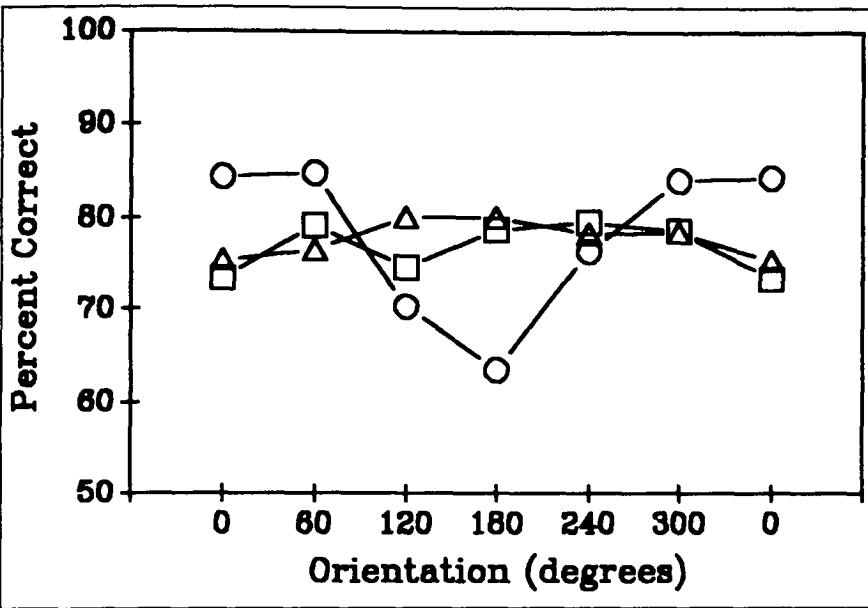


Fig 2 Percentage of correct responses for each eccentricity and orientation. Circle = 0° eccentricity, square = 4° eccentricity, triangle = 8° eccentricity

entation × Visual Half-Field interaction,  $F(5, 15) = 5.53, p < .005$ . 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 (Sergent & Corballis, 1989). For the right-visual-field (RVF) presentations, 83% of the variance was accounted for by this optimal mental rotation curve,  $F(1, 4) = 19.1, p < .02$ . 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.

### VALIDATION OF THE PARADIGM WITH HUMANS

For comparative purposes, we decided to test 3 human subjects with the same apparatus. The testing conditions were similar to those used with the baboons, except that humans sat in a chair and received two test sessions rather than four. The two sessions corresponded to Test Sessions 1 and 2 employed with the baboons. Humans proved to be highly accurate (89.9%, 89.5%, and 86.8% correct). For brevity, we do not consider accuracy data further, but rather focus on response times.

For the lateralized presentations, a significant main effect was found for orientation,  $F(5, 10) = 7.48, p < .005$ . The mean response times as a function of orientation and visual half-field are depicted in Figures 4a and 4b. An optimal mental rotation curve fit both LVF,  $F(1, 4) = 35.74, p < .005$ , and RVF,  $F(1, 4) = 18.11, p < .05$ , presentation data and accounted for 90% and 82% of the variance, respectively. Regarding the 0° eccentricity data, a significant orientation effect was also found,  $F(5, 10) = 5.55, p < .05$ , and the optimal rotation curve accounted for a significant proportion (89%) of the variance,  $F(1, 4) = 32.74, p < .005$ .

There are two additional noteworthy points of comparison. First, overall, the baboons responded more than twice as fast as the humans ( $M = 433$  ms vs  $M = 1,089$  ms). Second, there were differences in the rate of mental rotation between the two species. For every 60° rotation, the average increment in re-

Table 1 Mean response times (in ms) for each subject as a function of orientation and visual half-field

Degree of orientation	Right visual half-field				Left visual half-field			
	Subject 1	Subject 2	Subject 3	Subject 4	Subject 1	Subject 2	Subject 3	Subject 4
0	292	406	500	291	514	491	725	334
60	313	392	497	246	403	404	650	303
120	356	387	541	429	365	403	705	306
180	440	429	595	362	418	389	672	280
240	397	399	581	311	421	435	831	315
300	293	403	518	260	455	491	671	265

## Mental Rotation in Baboons

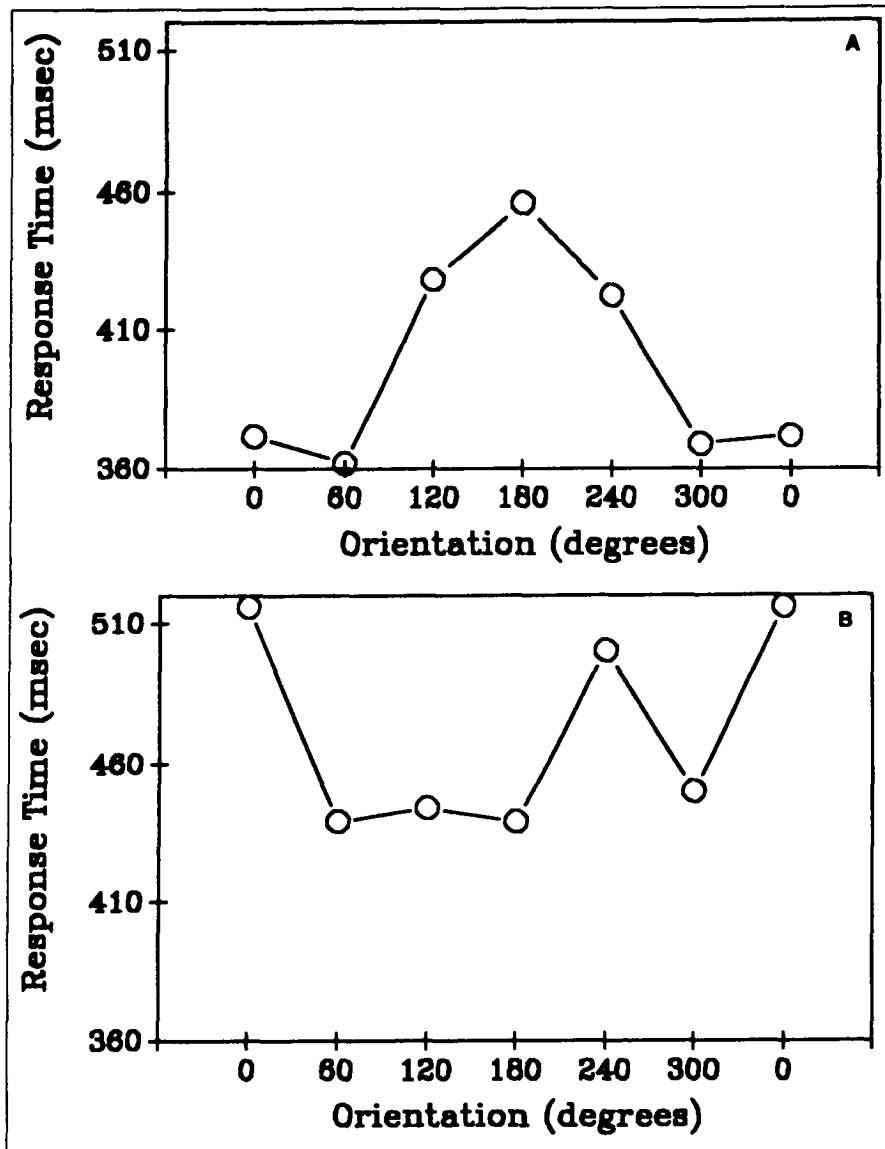


Fig 3 Baboons' response times as a function of orientation for stimuli displayed in the right visual half-field (a) and in the left visual half-field (b)

sponse 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 (Corballis & Beale, 1976). In the present study, we have demonstrated that baboons are capable of mirror-image dis-

criminations despite spatial transformations involving various disorientations (Fig 2). Additionally, contrary to the study with pigeons (Hollard & Delus, 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 discrep-

ancy 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 (Corballis & 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, Cowey, & Weiskrantz, 1984), although it is not entirely consistent with human findings (Sergent & Corballis, 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-

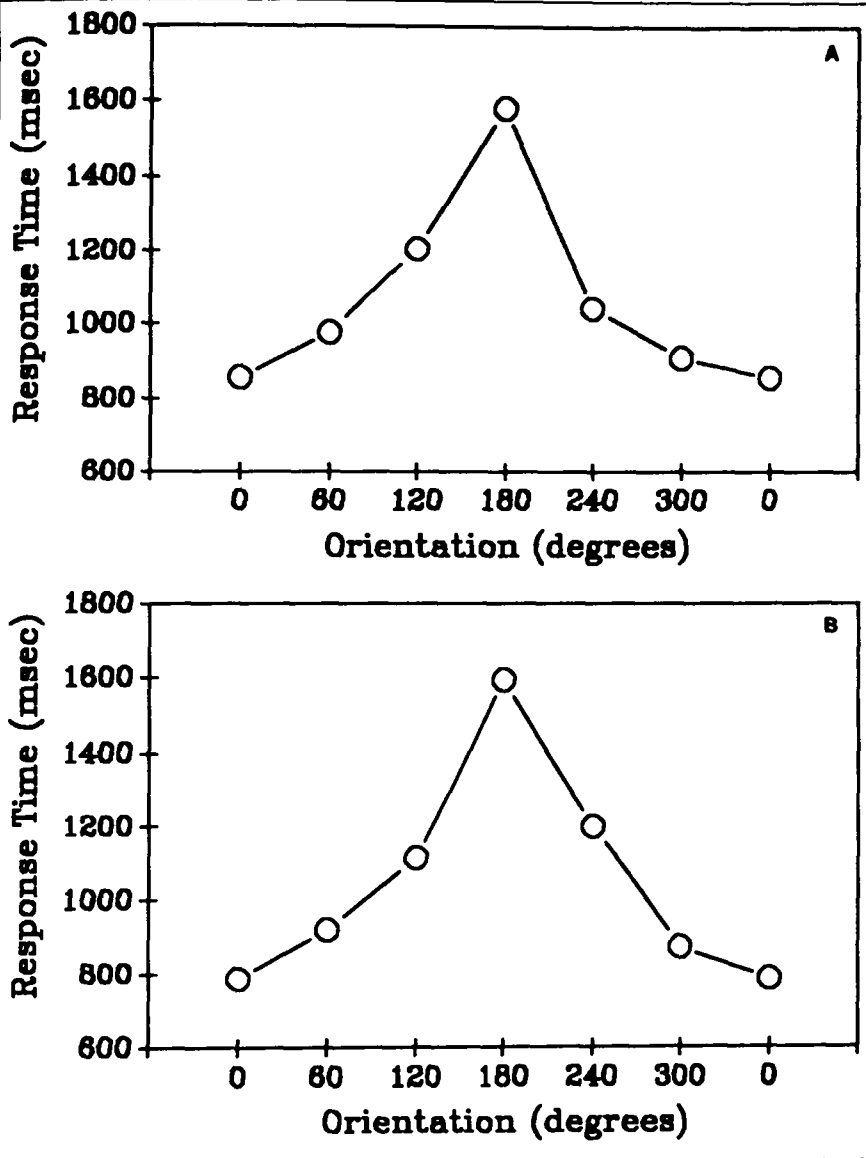


Fig 4 Humans' response times as a function of orientation for shapes presented in the left visual half-field (a) and in the right visual half-field (b)

ferences in the sensorimotor systems, or differences in cognitive levels of processing between the two species

In conclusion, the data provided here constitute the first demonstration of mental rotation for visual imagery in animals. Given the restricted stimulus pool used in this study, this effect needs to be investigated further. If these findings are replicated, the existence of mental rotation will suggest that this phenomenon has a common underlying cognitive basis in humans and baboons.

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