Mirror-Image Matching and Mental Rotation Problem Solving by Baboons (*Papio papio*): Unilateral Input Enhances Performance

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Three experiments, using a matching-to-sample procedure, were conducted to examine hemispheric specialization in mirror-image discrimination and mental rotation in baboons (*Papio papio*). In Experiment 1, no significant difference was found in discrimination of mirror-image and asymmetric pattern stimuli. In Experiment 2, orientation discrimination was assessed within the left (LVF) and right (RVF) visual half-fields. An RVF advantage was found in accuracy for asymmetric patterns, whereas an LVF advantage was found for discrimination of mirror-image stimuli. No significant relation was found between angular disparity of the stimuli and response time. Experiment 3 examined the effect of bilateral visual input on accuracy and response time. Significantly lower accuracy and longer response times were found for bilateral compared with unilateral visual input.

Mental rotation has been extensively studied in human subjects through a variety of different procedures and stimuli (see Shepard & Cooper, 1982, for review). In the typical mental rotation task, subjects are presented with a target stimulus followed by two or more comparison stimuli rotated in various angular degrees. The subjects are asked to match the target and one of the comparison stimuli. Usually, the comparison stimuli are mirror images of each other, such as the letter *p* and its left–right mirror image *q*, so that subjects cannot respond on the basis of the form features of the comparison stimuli. One general finding from these studies is a significant relation in reaction time between recognition of the target stimulus and degree of orientation of the comparison stimuli. Thus, on an incremental scale of 30° for a range of 0° to 180° orientations, reaction times are generally longer on trials with 180° orientations than on trials with orientations of 150°, 120°, 90°, 60°, or 30°. One

of a number of interpretations (Anderson, 1978; Kosslyn, 1980; Pylyshyn, 1973) for these findings is that human subjects create a mental image of the target stimulus and must rotate the target stimulus to the corresponding orientation until a match is found. Hence, with larger degrees of orientation, more time is needed to rotate the stimulus and respond correctly.

A second use of the mental rotation paradigm has been in the assessment of neuropsychological processes in human subjects (see Kosslyn, 1987). The two cerebral hemispheres have been characterized as having unique specializations in processing different types of stimuli. The right hemisphere has been characterized as being specialized for nonverbal, parallel, gestalt processing, whereas the left hemisphere is characterized as the verbal, sequential, analytic, or linguistically competent hemisphere (see Bradshaw & Nettleton, 1981, for review). Given the high spatial demands of the mental rotation task, it was thought that significant right-hemisphere effects would emerge from this paradigm, a finding that has often been supported (for review, see Ratcliff, 1979). However, some researchers have reported left-hemisphere advantages in this task (Corballis & Sergent, 1989). One possible explanation for differences in direction of laterality may be the type of stimuli used in the study. For example, using letters such as *p* and *q* enhances the left-hemisphere advantage because presumably the subjects are able to use a linguistic strategy to solve the task. Irrespective of the direction of asymmetries, the mental rotation paradigm seems to elicit hemispheric specialization in human subjects.

Given the recent interest in animal cognition (Roitblat, 1987; Roitblat, Bever, & Terrace, 1984) and discussion of representational or imagery processes in animals (Neiworth & Rilling, 1987; Roitblat, 1980), it would seem that the mental rotation paradigm would be an appealing approach for comparative studies of cognition and representation. Despite this appeal, to our knowledge there is only one published study that examined mental rotation in a nonhuman species (Hollard & Delius, 1982). By use of a matching-to-sample (MTS) task, pigeons were trained to discriminate mirror-image stimuli. Subsequently, the pigeons

received training on orientation matching with mirror-image stimuli. In the final test, the pigeons' performance on mirror-image stimuli with previously untrained orientations was assessed. For comparison, human subjects were also tested. The results indicate that both humans and pigeons were able to perform at comparable accuracy levels. However, the human subjects displayed the classic relation between orientation and choice reaction time. In contrast, the pigeons responded faster than human subjects but displayed a flat, nonsignificant relation between orientation and reaction time.

Hemispheric specialization in animals has never been assessed by means of a mental rotation paradigm. However, there is some evidence that nonhuman primates required to perform visual–spatial discriminations exhibit functional lateralization (e.g., Hamilton, 1983; Hamilton & Vermeire, 1988; Hopkins & Morris, 1989; Jason, Cowey, & Weiskrantz, 1984). For example, Hamilton (1983) taught split-brain monkeys oblique line discriminations differing in orientation by 15°. This discrimination was learned significantly faster when input was restricted to the left hemisphere than when input was restricted to the right hemisphere. One potential reason for the lack of mental rotation studies in nonhuman species is the prerequisite of accurate mirror-image discrimination and the apparent difficulties encountered by nonhuman animals for these types of learning problems (see Corballis & Beale, 1976, for review). Mirror-image discrimination problems preclude the use of the features within a stimulus as discriminative cues, as is the case in typical pattern discrimination problems (Sutherland, 1968). For example, Riopelle, Rahm, Itoigowan, and Draper (1964) presented monkeys with a series of two-choice discrimination problems involving planimetric stimuli that differed on a variety of perceptual dimensions, including stimuli that were mirror images. The most difficult discriminations were with the mirror-image stimuli. Similar data have been reported in chimpanzees (Nissen & McCulloch, 1937), monkeys (Brown & Ettlinger, 1983; Ettlinger & Elithorn, 1962), bushbabies (Sanford & Ward, 1986), cats (Warren, 1969), and pigeons (Lohmann, Delius, Hollard, & Friesel, 1988; Todrin & Blough, 1983). However, not all studies with pigeons have reported difficulties in learning mirror-image discriminations (Weiss & Hodos, 1986).

Studies using different procedures, such as the MTS procedure, have generally supported the conclusion that mirror-image stimuli are more difficult to discriminate than asymmetric patterns. Such results have been reported in chimpanzees (Matsuzawa, 1990) and in rhesus monkeys (Hamilton, Tieman, & Brody, 1973; Hopkins & Washburn, 1989), but not in pigeons (Hollard & Delius, 1982).

With respect to the successful study on mirror-image MTS in pigeons by Hollard and Delius (1982), we should point out that the pigeons in that study were trained in the MTS task by the use of mirror-image stimuli but not asymmetric patterns. Consequently, the pigeons' relative performance in the MTS task on mirror-image and pattern discriminations remains unclear. The data on two-choice discrimination learning in pigeons (e.g., Lohmann et al., 1988) are difficult to interpret with respect to the findings

obtained using an MTS procedure. Still, in the study by Hopkins and Washburn (1989), rhesus monkeys were unable to successfully match mirror-image stimuli, whether such stimuli were presented as a single stimulus set intermixed with pattern-matching problems or the task required sequential or simultaneous matching. These failures were encountered even though the subjects were able to successfully discriminate mirror-image stimuli presented as two-choice discrimination problems. Similar results have been reported in a chimpanzee (Matsuzawa, 1990).

There are at least three hypotheses for the apparent confusion of mirror-image stimuli in nonhuman animals. One theory suggests an anatomical basis for this problem (Noble, 1966; Orton, 1937). In this theoretical account, homotopic representation between homologous regions of the two cerebral hemispheres creates mirror-image representations of the same stimulus. Confusion arises because each hemisphere has a different representation of the same stimulus, with each representation being the mirror-image of its opposite counterpart. Support for this theory has come from research with split-brain subjects, including monkeys, pigeons, and rats that were able to learn mirror-image discriminations faster than intact controls (Beale, Williams, Webster, & Corballis, 1972; Noble, 1966, Noonan & Axelrod, 1991). Additional support comes from research on the discrimination of oriented oblique lines (Beale, 1968; Mello, 1965). In these studies, pigeons viewing rotated oblique lines monocularly showed mirror-image equivalence when the opposite eye was tested. Thus, subjects trained to respond with the left eye to lines with an orientation of 30° will respond most accurately to lines with an orientation of 210° when tested with the right eye.

A second, and somewhat related, hypothesis involves hemispheric specialization (Corballis & Beale, 1976). In this framework, an organism that is symmetrical is unable to discriminate left from right. An assumption of this model is that asymmetry in the brain provides an internal reference point with respect to left and right discrimination. Thus, monkeys and other animals would be unable to discriminate left from right (Corballis & Beale, 1976) because their brain is presumably symmetrical. As noted previously, however, the assumption of functional symmetry in nonhuman primate brains has been challenged recently by a number of investigators (see Fagot & Vauclair, 1991; MacNeilage, Suddert-Kennedy, & Lindblom, 1987; Ward & Hopkins, in press, for reviews).

A third explanation for these findings may be a simple limitation of the identity-matching concept, such as that proposed by D'Amato, Salmon, and Colombo (1985), or some limitation in animals' ability to extract perceptual or relational information at a conceptual level (Premack, 1983). Animals' poor performance on mirror-image stimuli may represent a class of situations that reveal limitations in cognitive processes underlying identity matching. Although difficulties in performance are encountered for mirror-image stimuli when both two-choice discrimination and matching procedures are used, one difficulty in evaluating this explanation is that the MTS paradigm has seldom been used to assess mirror-image discrimination.

Experiment 1

A majority of studies on mirror-image discrimination have used two-choice discrimination problems (e.g., Todrin & Blough, 1983), but relatively few have used MTS procedures (e.g., Hamilton et al., 1973). Previous research has also shown that MTS for mirror-image stimuli takes considerably more trials to learn when compared with asymmetric pattern identity matching (Hamilton et al., 1973; Hopkins & Washburn, 1989; Matsuzawa, 1990), although not in pigeons (Hollard & Delius, 1982).

To examine whether monkeys could succeed in mental rotation problems involving mirror-image stimuli, first it was necessary to establish whether mirror-image identity matching was feasible in this species. Additionally, given our further interest in the use of mental rotation paradigms in the assessment of hemispheric specialization in nonhuman primates, our second focus in Experiment 1 was to establish whether monkeys could respond accurately under conditions of rapid stimulus presentation necessary for lateralized input (i.e., <150 ms; Bryden, 1982).

Method

Subjects

The subjects were 3 wild-caught baboons (*Papio papio*), housed within the animal facility at the Centre National de la Recherche Scientifique, Marseille, France. The weighed 9.8, 5.8, and 7.0 kg, respectively, and were estimated to be between 2.5 and 4.0 years of age. Prior to this series of experiments, the subjects had been trained on a psychomotor task involving the use of a joystick that controlled a cursor displayed on a computer monitor (Vauclair & Fagot, 1993) but had received no discrimination learning or MTS tasks. The subjects were housed in a social group with 11 other baboons but were removed from the group daily for training and testing and then returned to the group. The subjects were not deprived of food or water and were fed their daily ration of fruit,

vegetables, and chow and the end of each test session. Food was not accessible during testing except for food received as reinforcement during training or testing.

Apparatus

The apparatus used in this study has been described elsewhere (Vauclair & Fagot, 1993). In brief, the main apparatus was comprised of (a) an IBM-compatible AT 286 microcomputer, (b) an accompanying 14-inch color monitor, (c) an analog joystick (Measurement Systems model 521) controlled by an analog–digital converter (data translation board from Data Translation, Inc.), and (d) a food dispenser for 190-mg pellets (P. J. Noyes). The testing environment also included a 68 × 50 × 72 cm experimental cage, as shown in Figure 1. The cage had a view port (8.7 × 8.0 cm) and two hand ports in the panel facing the computer monitor. The distance from the view port to the computer monitor was 47 cm. The center of the computer monitor was aligned with the center point of the view port. The hand ports could be opened or closed by sliding panels to restrict joystick manipulation to either the left or right hand. The joystick was positioned 18 cm from the hand ports and was centrally positioned on the horizontal axis of the experimental cage. Also centrally positioned on the horizontal axis, but 5 cm from the hand ports, was a touch-sensitive pad measuring 11.5 × 10.0 cm. A specific software program was developed for this study and was written in Turbo Pascal 5.0. Timing of stimulus presentation and recording of response times were controlled by a digital–analog board (Data Translation DT2801) with a 1-ms sampling rate.

Procedure

MTS training. During all training and testing, each subject was separated from the group and placed in the experimental cage. Subjects initiated a trial by placing a hand on the touch pad. Immediately thereafter, the cursor would appear in the center position of the computer monitor. The cursor was always a green circle 0.5 cm in diameter. In addition to the cursor, a target stimulus appeared at one or more positions on the computer monitor
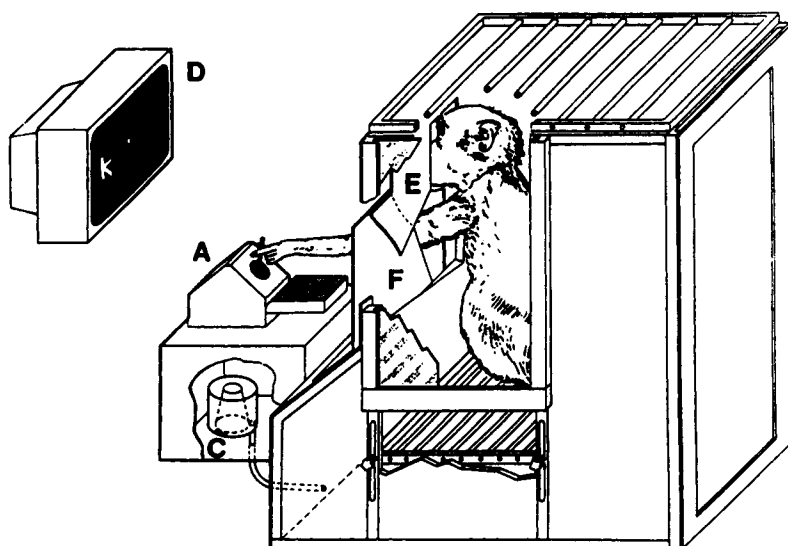

Figure 1. Test apparatus used in this study. (A = joystick; B = touch pad; C = food dispenser; D = computer monitor; E = view port; F = hand port.)

(depending on the phase of training). The subjects were required to manipulate the joystick so as to direct a collision between the cursor and the target stimulus. If this condition was met, two comparison stimuli appeared at a specific location on the monitor. The subjects were then required to direct a collision between the cursor and one of the two comparison stimuli. A correct response was recorded when the subjects touched the comparison stimulus matching the target stimulus with the cursor. An incorrect response was recorded when the subjects touched the comparison stimulus different from the target stimulus with the cursor. All correct responses were reinforced with a 190-mg food pellet and an accompanying tone.

Incorrect responses were followed by a low, raucous tone and a time-out (TO) varying from 5 to 20 s. The intertrial interval (ITI) varied from 1 to 15 s. During the TO or ITI, the computer screen turned green. At the end of the TO or ITI, the screen was black. If subjects were either moving the joystick or holding their hands on the touch pad before the TO or ITI terminated, the initiation of the next trial was delayed until the subjects removed hands from the touch pad and the joystick was in the central position. During all training and testing, the subjects used the same hand to manipulate the joystick. One subject (a male) used the right hand, and 2 used their left hands (1 male and 1 female). The hand used to manipulate the joystick was randomly assigned and was determined on the basis of previous experiments examining manual specialization in these same subjects (Vauclair & Fagot, 1993).

Training on MTS was done in four phases. Mastery at any phase of training required greater than 80% accuracy across the course of 150 trials. In Phase 1, after initiating the trial, the target stimulus was presented laterally 5 to 10 cm from the cursor. The position of the target stimulus was always presented in the horizontal median axis of the screen. The subjects were required to sample the target stimulus by directing a collision between the cursor and the target stimulus, at which point two comparison stimuli appeared. The position of the comparison stimuli was randomly determined but was constrained to six different positions, three in the upper half and three in the lower half of the screen. The target stimulus stayed visible throughout the trial.

In Phase 2, the task was similar with respect to the position and sampling requirements of the target stimulus. However, the presentation of the comparison stimuli was restricted to either the top or bottom half of the monitor. In other words, one comparison stimulus appeared in the top half, and the other appeared in the bottom half. Also during Phase 2, color was removed as a discriminative cue, such that the stimuli appeared in only one color within a test session. This was done to ensure that subjects were matching on the basis of the pattern of the stimulus rather than any color features. In Phase 3, two changes were made. First, after sampling on the target stimulus, the comparison stimuli appeared in two fixed positions. These two positions were located on the central vertical axis on the bottom or top of the screen. Secondly, the target stimulus was removed from the screen after the sampling response. In other words, the task became a sequential rather than a simultaneous MTS task.[1] In Phase 4, a sampling response was no longer necessary, and the target was presented for a limited duration, at which point the comparison stimuli appeared and the target disappeared.

Introduction of the fixation response and reduced durations of unilateral presentation of the target stimuli commenced once subjects had mastered the Phase 4 training. This training was somewhat similar to that used by Hopkins, Washburn, and Rumbaugh (1990). As with the previous training, a trial was started by having the subjects place their hands on the touch pad. The cursor appeared at its central location on the monitor; however, rather than having the target stimulus appear, the fixation stimulus was displayed at a location 1.5 cm above or below the cursor. The fixation stimulus was a white square measuring 0.5 cm × 0.5 cm. The subjects had to place the cursor in the exact center of the fixation point for 25 ms, at which point the target stimulus appeared either to the left or right of the fixation stimulus (a visual angle of 6°). The presentation duration of the target stimulus was initially 1,000 ms. The presentation duration was reduced systematically until subjects' correct response rate was 80% or better over the course of 150 trials with a presentation duration of 150 ms.

During initial training, we sought to maximize the variability in stimuli so as to facilitate acquisition of MTS. This was done by using a wide range of pattern and colored stimuli. The stimuli used during initial training were color stimuli of various shapes but with a maximum size of 2.2 × 2.2 cm. The stimuli were generated by a computer program written in PASCAL and used the available graphic functions within this computer language. These included stimulus patterns such as circles, lines, squares, triangles, arcs, and rectangles. Additionally, at least in the preliminary training, 15 different colors were used in conjunction with the different stimulus patterns.

Testing procedure. Each subject received 640 trials, presented as two series of four 80-trial test blocks. In the first series of 4 test blocks, the stimuli consisted of geometric patterns (2.2 × 2.2 cm) composed of the 255 ASCII characters on any standard computer keyboard, such as letters, punctuation marks, or numbers (e.g., *H*, &, , *, and 2). Two sets of 10 novel asymmetric pattern stimuli were used in the first series of 4 blocks of testing. In Blocks 1 and 2, the first set of 10 novel stimuli was used. In Blocks 3 and 4, 10 different novel stimuli were used. Within a block of 80 trials, each stimulus was presented eight times, four times to each visual half-field, with the positive comparison stimulus appearing in the top or bottom position on 2 trials. The incorrect comparison stimulus (referred to as the *foil*) was pseudorandomly selected from among the remaining 9 stimuli comprising each stimulus set.

In the second series of four test blocks, mirror-image stimuli were used. All mirror-image stimuli were left–right mirror-image comparisons (e.g., [vs.]). As with the geometric patterns, two sets of 10 mirror-image stimuli were used. One set of 10 stimuli was used in Blocks 1 and 2, whereas 10 novel mirror-image stimuli were used in Blocks 3 and 4. Within a block of 80 trials, each stimulus was presented eight times, four times to each visual half-field, with the positive comparison stimulus appearing in the top or bottom position on 2 trials. The incorrect comparison stimulus (or foil) was always the mirror image of the correct stimulus.

We should emphasize that for both sets of stimuli, the correct response required the subjects to perform identity matching. The difference between the two stimulus sets was in the type of foil stimulus. In the case of asymmetric patterns, the foil was a different asymmetric pattern from the target stimulus. For mirror-image stimuli, the foil was the left–right mirror image of the positive target stimulus.

To prevent overlap in the visual meridian and to assure unilateral presentation of the stimuli, the inside edges of the stimuli were displaced to the left or right of the fixation stimulus by 6°.

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[1] Because of the experimental paradigm we are using, there is a slight delay between target stimulus offset and the presentation of the comparison stimuli. This delay is due to the clearing of computer screen between target and comparison stimulus presentations. This delay varies between 8 and 20 ms and is not detectable by human observers.
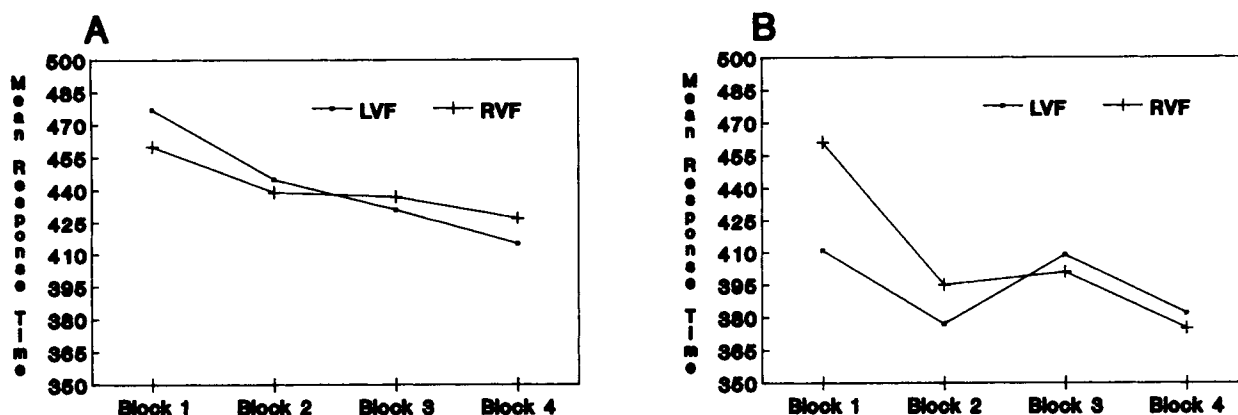
Figure 2. Mean response time in Experiment 1 as a function of block and visual half-field for asymmetric pattern stimuli (A) and mirror-image stimuli (B). (LVF = left visual half-field; RVF = right visual half-field.)

Furthermore, presentation duration of the target stimulus was 100 ms, a value considered adequate for unilateral input (Bryden, 1982). Both accuracy and response time served as dependent measures. Response time was measured as the time elapsed between the offset of target stimulus presentation and the detection of a collision between the cursor and comparison stimulus.

Results

Because of the possibility that the subjects could anticipate a response or experience some difficulty in responding within a trial (for any number of reasons, such as inattention because of distraction), some data reduction was performed. For each subject, mean response times were calculated for each stimulus set, and any individual data point that exceeded 3 standard deviations from this mean was removed from the data set. Also, response times less than 100 ms were removed because of the high probability that they reflected anticipation responses. This procedure reduced the total data set by less than 2%. For all significant main effects and interactions (those that exceeded $p < .05$), post hoc analyses were performed using Tukey's honestly significant difference (HSD).

Mean accuracy and response time for each subject were analyzed using a complete within-subjects analysis of variance (ANOVA). The independent variables of interest included stimulus set (asymmetric pattern vs. mirror image), test block (1, 2, 3, or 4), and visual half-field (LVF or RVF). For accuracy, no significant main effects or interactions were found. Overall accuracy was 79% for pattern stimuli and 78% for mirror-image stimuli. In terms of response time, the only significant effect was a three-way interaction between stimulus set, block, and visual half-field, $F(3, 6) = 4.52$, $p = .05$. Note that this effect was only marginally significant. The mean response times for this interaction effect can be seen in Figure 2, parts A and B. Post hoc analyses indicated that RVF response times were significantly faster than LVF responses for asymmetric patterns only within Block 1. In contrast, LVF response times were significantly faster than RVF response times for

mirror-image stimuli within Block 1 as well as Block 2. No visual half-field differences were found in Blocks 3 and 4.

Discussion

The data from Experiment 1 indicate that baboons were able to match mirror-image stimuli as reliably as asymmetric patterns, despite a presentation duration of 100 ms. Because the presentation of mirror-image stimuli was essentially a test of generalization of matching abilities from asymmetric pattern to mirror-image stimuli, it can be concluded that generalization was at a high level, because no significant effects were found for the block or stimulus-set variables. Mean accuracies for the mirror-image stimuli were 78%, 78%, 81%, and 74% for Blocks 1 to 4, respectively, revealing quite consistent performance.

In terms of accuracy, our data are not consistent with previous findings on mirror-image discrimination in nonhuman primates derived using an MTS paradigm (Hamilton et al., 1973; Hopkins & Washburn, 1989; Matsuzawa, 1990). In these studies, performance on mirror-image problems was either significantly worse or took more trials to reach criterion than asymmetric patterns. In contrast, our subjects experienced little difficulty in responding correctly to the mirror-image stimuli, even on their initial experience with these stimuli. Therefore, it seems unlikely that failure to show significant MTS for mirror-image stimuli represents a limitation of the matching concept in monkeys (D'Amato et al., 1985). One possible explanation for these differences may be the learning history of the subjects in each study; that is, subjects may have been overtrained. For example, the chimpanzee studied by Matsuzawa (1990) was trained in an artificial communication system using geometric forms representative of words (Matsuzawa, 1985). This chimpanzee was likely overtrained on MTS that focused on recognition of asymmetric patterns. Likewise, the monkeys studied by Hopkins and Washburn (1989) had received extensive behavioral testing, including psychomotor tasks, discrimination learning, mediational learning, delayed

matching, and same–different discrimination, prior to testing with mirror-image stimuli (see Washburn, Hopkins, & Rumbaugh, 1989a, 1989b, 1991). In contrast, our baboons were relatively naive for behavioral testing prior to this study. For example, once they had mastered the basic joystick task, MTS training commenced without other intervening behavioral tests.

An alternative explanation for the successful mirror-image matching may involve the unilateral presentation of stimuli. For example, because our subjects were neurologically intact, there should have been bilateral representation of the stimuli and thereby confusion, at least according to the theoretical model forwarded by Noble (1966). Split-brain monkeys (Noble, 1966) and rats (Noonan & Axelrod, 1991) can learn mirror-image discriminations faster than intact controls. The presumed reason is that the homotopic pathways would be unable to project contralaterally because the interhemispheric pathways are cut. In pigeons, under conditions where the subjects must use interhemispheric communication pathways, mirror-image discrimination learning is compromised (Weiss & Hodos, 1986). Finally, monkeys with their optic chiasms cut and with training in matching mirror-image and asymmetric pattern stimuli show better performance when the task requires intrahemispheric matching compared with interhemispheric matching (Hamilton et al., 1973).

By way of divided visual-field presentation, we presented both asymmetric and mirror-image stimuli unilaterally to each hemisphere, and therefore it might be suggested that by precluding overlap in the visual meridian, we effectively restricted information to one cerebral hemisphere. In this sense, at least on initial stimulus presentation, only one hemisphere was receiving input of the visual stimulus, and there was limited dual representation of the stimulus.

Regarding response time data, the largest differences between visual half-fields were found in Block 1. For the asymmetric patterns, an RVF advantage was found, whereas an LVF advantage was found for the mirror-image stimuli. However, because the interaction was borderline significant, these data should be interpreted cautiously. Moreover, the visual-field effects as a function of stimulus set dissipated with repeated testing. Although it could be argued that the visual half-field effects in Block 1 were due to the novelty of the stimuli (Goldberg & Costa, 1981), such an explanation does not seem likely. If novelty were the only relevant factor, then the direction of asymmetry should have been the same for both stimulus sets. A more likely explanation may be different perceptual treatment of the stimuli by our subjects. Specifically, the asymmetric patterns differed with respect to their general shape as well as the details comprising these stimuli. In contrast, the mirror-image stimuli were different only in their lateral orientation. It could be argued that the asymmetric patterns were discriminated on the basis of their focal components, whereas the mirror-image stimuli were distinguished on the basis of their contours. These types of distinctions have been shown to differentially involve the right and left hemispheres in human subjects (Bradshaw & Nettleton, 1981).

Experiment 2

Because the results from Experiment 1 indicated that our subjects could reliably match both asymmetric patterns and mirror-image stimuli with no significant difference in accuracy, in Experiment 2 we focused on the effect of stimulus orientation on accuracy and response time. Whether the use of mirror-image stimuli is necessary to find a relation between orientation and reaction time has been debated. Some have reported a flat reaction time curve in recognition of asymmetric patterns rotated at various angles (White, 1980), whereas others have reported significant curves between reaction time and orientation (Jolicoeur & Landau, 1984; Jolicoeur, Snow, & Murray, 1987; Sergent & Corballis, 1989), although the slopes of the curves were different from the typical mental rotation findings (Cooper & Shepard, 1973). For example, Sergent and Corballis (1989) reported that the reaction time slope for faces rotated 0° to 300° was 7,500° per second. In contrast, with mirror-image stimuli rotation per second ranges from 300° to 600° (Shepard & Metzler, 1988). Thus, even in the recognition of rotated asymmetric patterns, some variability as a function of angular disparity is found.

Whether mirror-image or asymmetric pattern stimuli can elicit mental rotation processes in animals is unknown. Therefore, we assessed recognition of rotational invariance, using both asymmetric patterns and mirror-image stimuli. If subjects were using a rotation strategy, we anticipated that response times would be slower as a function of greater angular disparity. Additionally, on the basis of the literature on humans (Corballis, 1988), if mirror-image discrimination is presumably more difficult than asymmetric patterns, then the slope in response time should be greater for the mirror-image stimuli than for asymmetric patterns.

Method

Subjects and Apparatus

The same subjects and apparatus as those in Experiment 1 were used in this experiment.

Procedure

The general testing procedure was similar to that used in Experiment 1. To initiate a trial, subjects were required to place their hands on the touch pad, at which point the cursor and the fixation stimulus appeared on the computer screen. Subjects then had to manipulate the joystick so as to place the cursor within the confines of the fixation stimulus for 25 ms, at which point a target stimulus appeared in either the LVF or RVF at a visual angle of 6° for 100 ms. After target stimulus presentation, two comparison stimuli appeared at the bottom and top horizontal axes of the computer monitor. An up or down response to designate the comparison stimulus matching the target was required to indicate a correct response. Positive responses were reinforced with food.

Two sets of stimuli were used in this study. The first stimulus set was composed of the letters F, R, P, and K. The second set of stimuli consisted of two additional ASCII characters (but not letters) and their mirror-image counterparts. The stimuli measured a maximum of 2.2 × 2.2 cm and were yellow. An example of the stimuli

comprising the two different stimulus sets and their differing orientations is shown in Figure 3. The upper panels show an asymmetric pattern problem, and the lower panels show a mirror-image problem. The left panels show the target stimulus presentations and the right poncis depict the displays during the presentation of the comparison stimuli. An upward movement was the correct response for the asymmetric pattern problem, and a downward movement was the correct response for the mirror-image problem.

A total of 448 trials were presented to each subject. Subjects were tested on 224 trials composed of two test blocks of 112 trials for each stimulus set. The letters comprising the first stimulus set were presented in Test Blocks 1 and 2, and the mirror-image stimuli were presented in Test Blocks 3 and 4. Within a 112-trial test block, each stimulus was presented 28 times, 14 each to the LVF and the RVF. Of these 14 trials, the position of the correct stimulus was pseudorandomly selected on either the top or bottom for 7 trials. Of these 7 trials, the comparison stimuli were oriented in one of the seven possible orientations (0°, 30°, 60°, 90°, 120°, 150°, or 180°). The target stimuli were always presented in their 0° orientation. Both comparison stimuli were oriented the same number of degrees, but the degree of orientation differed between trials. As with Experiment 1, the dependent measures included accuracy and response time. Independent variables of interest included stimulus set (asymmetric patterns or mirror images), block (1 or 2), orientation (0°, 30°, 60°, 90°, 120°, 150°, or 180°), and visual half-field (LVF or RVF).

Results

Table 1 shows mean accuracy and response time as a function of stimulus set, block, orientation, and visual half-field. As in Experiment 1, response times that exceeded 3 standard deviations within each possible orientation were excluded from analysis. Additionally, any response times below 100 ms were excluded because of the high probability they were anticipation responses. This data-reduction technique resulted in a loss of 1.6% of the overall data.

A complete within-subjects ANOVA of the accuracy data revealed a significant main effect for stimulus set, $F(1, 2) =$
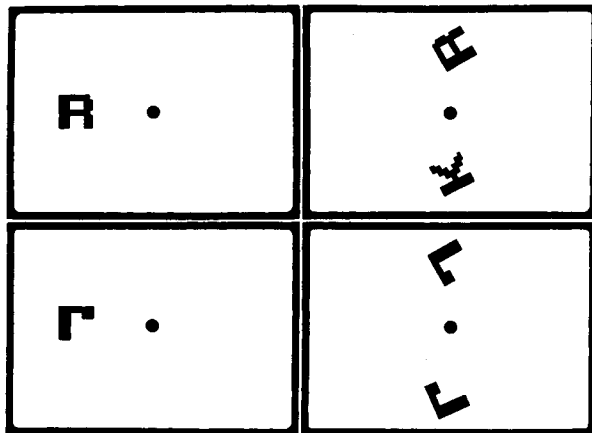

Figure 3. Examples of asymmetric (upper panels) and mirror-image stimuli (lower panels) rotated 60°. (The two left panels depict the display during stimulus presentation. The two right panels depict the display when the two comparison stimuli appeared on screen. In these examples, the correct response is an upward movement for asymmetric patterns and a downward movement for the mirror-image problem.)

Table 1

Mean Accuracy and Response Time (RT) as a Function of Stimulus Set, Block, Orientation, and Visual Half-Field (Experiment 2)

Orient	Field	Patterns rotated %C	Patterns rotated RT	Mirror-image rotated %C	Mirror-image rotated RT
		Block 1			
0	Right	58	418	79	579
30		81	373	67	439
60		79	409	71	412
90		72	410	79	413
120		72	456	83	536
150		76	365	92	393
180		74	419	79	367
0	Left	83	332	79	455
30		82	415	88	416
60		85	355	83	387
90		71	394	67	413
120		75	414	75	537
150		83	413	75	409
180		83	435	63	365
		Block 2			
0	Right	88	448	67	372
30		100	362	75	396
60		96	355	58	322
90		88	390	50	415
120		75	378	54	361
150		92	353	67	386
180		88	449	79	369
0	Left	83	398	71	364
30		79	374	75	316
60		92	367	79	334
90		79	403	71	329
120		88	470	75	389
150		92	376	71	388
180		71	373	75	386

Note. RT values are given in milliseconds. Orient = orientation in degrees; Field = visual half-field; %C = percentage correct.

93.63, $p < .02$, and orientation, $F(6, 12) = 4.78, p < .01$. Two 3-way interactions were significant, Stimulus Set × Block × Visual Half-Field, $F(1, 2) = 25.13, p < .04$, and Stimulus Set × Block × Orientation, $F(6, 12) = 4.78, p < .05$. Figure 4 shows mean accuracy as a function of stimulus set, block, and visual half-field. Post hoc analyses (HSD) indicated that RVF accuracy within Block 2 for asymmetric patterns was significantly greater than RVF accuracy in Block 1. In contrast, RVF responses in Block 2 for mirror-image stimuli were significantly worse than in Block 1. Additionally, within Block 2, mean accuracy for RVF presentations with mirror-image stimuli was significantly worse than for RVF presentations with asymmetric patterns. Thus, from Block 1 to Block 2, RVF accuracy became better for asymmetric patterns but worse for mirror-image stimuli. No other post hoc comparisons were significant. For the 3-way interaction between stimulus set, block, and orientation, subjects clearly performed better on the patterns from Block 1 ($M = 77\%$) to Block 2 ($M = 86\%$). In contrast, performance on mirror-image stimuli decreased from
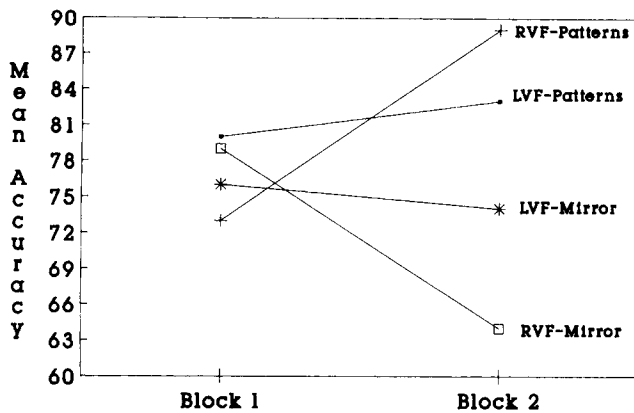
Figure 4. Mean accuracy as a function of block, stimulus set (asymmetric patterns or mirror-image stimuli), and visual half-field (Experiment 2). (RVF = right visual half-field; LVF = left visual half-field.)

Block 1 (*M* = 77%) to Block 2 (*M* = 69%). This effect was enhanced for orientations of 60°, 90°, and 120° (see Table 1).

With respect to the response time data, a within-subjects ANOVA failed to reveal any significant main effects or interactions. Trend analysis on the slope of the response time measures as a function of orientation failed to show a significant linear, $F(1, 5) = .067$, $p > .10$, quadratic, $F(1, 5) = .072$, $p > .10$, or cubic, $F(1, 5) = 3.70$, $p > .10$, trend. However, trend analyses applied to each stimulus set revealed a significant cubic trend for the mirror-image stimuli, $F(1, 5) = 8.27$, $p < .04$, which accounted for 62% of the variance. No significant trends were found for the asymmetric pattern stimuli.

Discussion

Analyses of accuracy data revealed slightly better performance for asymmetric patterns compared with mirror-image stimuli presented in 0° orientations and matched to rotated comparison stimuli ranging from 30° to 180°. This was particularly true at rotations of 60°, 90°, and 120°. This effect was enhanced with continued testing and when the asymmetric pattern stimuli were presented to the RVF. Analysis of the response time data revealed no significant main effects or interactions.

It is clear from this experiment that the baboons were able to solve the mental rotation problem but did so by means of a different strategy than that used by human subjects (Cooper & Shepard, 1973). Support for this conclusion comes from the lack of a significant quadratic curve regarding response time data as a function of orientation. In this sense, it could be argued that our data are comparable to the previous data on pigeons and that the two species perhaps use similar strategies (Hollard & Delius, 1982). However, comparing the findings from our study with those of Hollard and Delius (1982) is difficult for a number of reasons. First, Hollard and Delius trained their pigeons to perform some rotational problems before they were tested on the mental rotation task. No such training was necessary in the baboons

from our study because performance was high from the onset of testing with the rotated mirror-image stimuli. We believe this is a significant difference between the two studies. Second, we tested our animals with rotated asymmetric and mirror-image stimuli, whereas Hollard and Delius only used mirror-image stimuli. Third, although accuracy was comparable between the two studies, our baboons responded much faster than the pigeons studied by Hollard and Delius. Specifically, as inferred from the graph presented by Hollard and Delius (1982, Figure 3A, p. 805), the mean reaction times for the pigeons they studied were 750 to 1,000 ms. For baboons, the mean response time was 402 ms for mirror-image stimuli. Despite these differences, it is clear that neither species showed a strong and predictable slope between response time and angular disparity.[2]

As mentioned in Experiment 1, we believe one important reason why the baboons were able to perform significantly above chance, to respond relatively quickly without specific training on rotation problems or mirror-image discriminations, resides in the unilateral presentation of stimuli. In other words, our hypothesis is that unilateral presentation was critical because the visual information was restricted (at least on initial presentation) to one cerebral hemisphere. To further explore this hypothesis, we performed a third experiment. In this experiment, processing of mirror-image stimuli and rotated mirror-image stimuli was examined under conditions where target stimulus input was not restricted to one visual half-field. On the basis of the perspective of homotopic representation (Noble, 1966), the hypothesis with respect to this experiment was straightforward. When the target stimulus is presented to both hemispheres, performance should be significantly worse than when the target stimulus is presented to one hemisphere.

Experiment 3

Method

The subjects, apparatus, and general procedure were identical with those used in Experiments 1 and 2. In this experiment, subjects were required to match simultaneous mirror-image stimuli as well as mirror-image stimuli presented at different orientations. The major difference in procedure from Experiments 1 and 2 was the presentation mode of the target stimulus. The target stimulus was presented laterally for 100 ms, followed by the appearance of the two comparison stimuli. In Experiments 1 and 2, the target stimulus disappeared when the comparison stimuli were displayed on the screen. In this experiment, the target stimulus stayed visible during the entire duration of the trial rather than disappearing from the screen. This procedure allowed subjects to inspect the stimulus by way of saccadic eye movements, which direct information to both hemispheres.

Four test blocks were performed. In Test Blocks 1 and 2, the first 10 mirror-image stimuli used in Experiment 1 were presented. In Test Blocks 3 and 4, the 4 rotated mirror-image stimuli used in Experiment 2, Blocks 3 and 4, were presented (See Figure 3).

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[2] Hollard and Delius (1982) reported that the maximum response times in their pigeons occurred at 90° rotations.

All subjects were first tested for mirror-image matching, followed by testing for orientation mirror-image matching. In Blocks 1 and 2, as with Experiment 1, 80 trials were presented. Each of the 10 stimuli was presented as the target stimulus on 8 trials, 4 trials each to the left and right of the fixation stimulus. On 2 trials, the correct comparison stimulus appeared in either the top or bottom position. In Test Blocks 3 and 4, the orientation mirror-image matching procedure was identical with that used in Experiment 2. Each test block was composed of 112 trials. On 56 trials, the target stimulus appeared to either the left or right of the fixation stimulus. Each of the 4 stimuli was presented on 14 trials, with 2 trials being presented at each of the seven orientations. Of these 2 trials, the correct target stimulus was in either the top or bottom position. As with Experiment 2, the target stimulus was always presented in the 0° orientation. The dependent measures were accuracy and response time.

Results

To assess the effect of this mode of presentation, the data from this experiment were analyzed with respect to the findings for the comparable stimulus sets in Experiments 1 and 2. Thus, for mirror-image matching, the data from Blocks 1 and 2 of Experiment 1 with mirror-image stimuli were analyzed with respect to the data collected in Blocks 1 and 2 of this experiment. In the case of the orientation mirror-image matching, the data collected in Blocks 3 and 4 of Experiment 2 were compared with the data collected in Blocks 3 and 4 of Experiment 3. For each stimulus set (mirror-image matching and mirror-image rotated stimuli), a complete within-subject ANOVA was performed, because the test procedures with respect to the number of trials and variables were the same between experiments. The variable visual half-field was irrelevant in this experiment because stimulus presentation by way of visual field was unrestricted. This variable was dropped from the analysis. The independent variables of interest were, therefore, experimental condition (unilateral vs. bilateral input) and Block (1 or 2) for the mirror-image stimuli. With respect to the mirror-image rotated stimuli, the independent variables were experimental condition (unilateral vs. bilateral input), block (1 or 2), and orientation (0°, 30°, 60°, 90°, 120°, 150°, or 180°).

Mirror-Image Matching

An ANOVA revealed no significant main effects or interactions for accuracy, (for unilateral, $M = 78\%$; for bilateral, $M = 75\%$). For response time, a significant main effect was found for experimental condition, $F(1, 2) = 95.64, p < .03$. Mean response time for unilateral input (411 ms) was significantly faster than mean response time for bilateral input (483 ms). No other effects reached significance.

Mirror-Image Orientation Matching

Regarding accuracy, a significant interaction was found between experimental condition and block, $F(1, 2) = 98.4$, $p < .04$. Mean accuracy in Block 1 for unilateral input (75%) was significantly higher than mean accuracy for bi-

lateral input in Block 1 (66%). Within Block 2, no significant differences in accuracy were found between unilateral input ($M = 75\%$) and bilateral input ($M = 74\%$). A significant main effect was also found for orientation, $F(6, 12) = 7.45, p < .03$. Mean accuracies as a function of orientation were 70%, 70%, 75%, 63%, 73%, 74% and 69% for rotated stimuli of 0°, 30°, 60°, 90°, 120°, 150°, and 180°, respectively. With respect to response time data, a within-subjects ANOVA failed to reveal any significant main effect or interaction. A trend analysis on the slope of the response time measures as a function of orientation failed to show any significant findings for linear, $F(1, 5) = 0.025, p > .10$, quadratic, $F(1, 5) = 0.35, p > .10$, or cubic, $F(1, 5) = 3.48, p > .10$, trends. There were no other significant effects.

General Discussion

The general results from these three experiments can be summarized as follows: (a) Baboons were able to match mirror-image stimuli without specific training, (b) asymmetric and mirror-image patterns were recognized when stimuli were presented for 100 ms, (c) baboons were able to recognize asymmetric patterns and mirror-image stimuli rotated 30° to 180° with comparable levels of performance, (d) no significant linear trend was found between response time and angular rotation of asymmetric patterns or mirror-image stimuli, and (e) bilateral visual input of mirror-image and mirror-image rotated patterns resulted in longer response times and poorer accuracy compared with unilateral visual input.

The lack of a relation between orientation and response time in these baboons relative to human subjects could reflect a number of different factors. One factor may be that these baboons focused on certain features of the stimuli as discriminative cues rather than focusing on their global form (Sutherland, 1968). Although such an explanation could account for the baboons' performance on asymmetric patterns, this explanation is less plausible with respect to the data on mirror-image stimuli. Alternatively, Corballis (1988) argued that mental rotation operates in the following manner. Subjects identify the stimulus, rotate the stimulus to the corresponding orientation, and then decide whether the stimulus is either in its normal or backward orientation. This latter process, referred to as the handedness or parity of the stimulus, is the dimension on which left–right mirror-image discriminations are made. It seems that the baboons, and probably the pigeons, were able to code the parity of the stimulus independent of stimulus orientation and most likely used this discriminative cue more than human subjects. However, for mirror-image stimuli rotated 180°, the parity is reversed. Thus, a simple parity rule cannot explain all of our data.

Adult humans have an image of what the letter F looks like in its normal orientation, and this knowledge may facilitate mirror-image discrimination. Support for this finding comes from data indicating faster reaction times to normally oriented letters compared with their mirror images (Corballis, 1982). The baboons had no sense of normal orientation for the stimuli we used (because they were nov-

el), and therefore they may have placed greater emphasis on other discriminative cues, such as the parity of a stimulus. In fact, there were no differences in the baboons' mean response times for stimuli presented in their normal orientations (by human standards) and their mirror images (normal = 365 ms; mirror = 384 ms). If this premise is true, then with sufficient familiarity with a stimulus and its normal orientation, rotation-type processes would emerge in the species under investigation. This reasoning, though, cannot account for Hollard and Delius' (1982) findings with pigeons, because the pigeons were trained and tested with the same set of stimuli.

Irrespective of which strategy the baboons used to respond correctly, it is clear that they used a similar strategy that was independent of the stimuli or task demands. This conclusion is supported by viewing the mean response times as a function of orientation and experiment presented, as shown in Figure 5. As the figure shows, the response time fluctuations were nearly identical, although the response times were slower for bilateral input than for unilateral input of either asymmetric patterns or mirror-image stimuli. Moreover, there was some variation in response time, particularly from 30° to 120° rotations. In fact, our data are very similar to those reported by Jolicoeur et al. (1987) with human subjects. In their study, reaction time in the identification of rotated letters increased up to the orientation of 120°. Between 120° and 180°, there was a reduction in reaction time. Why reduced reaction time is found at this rotation in both species remains unclear.

Regarding the problem of mirror-image discrimination, we believe we can offer at least a partial solution and a possible explanation. Simply stated, to obtain significant mirror-image discrimination performance, limit the presentation of information to one cerebral hemisphere. It is clear from the results of Experiments 2 and 3 that subjects could respond more quickly and more accurately, at least in Test Block 1, when stimuli were presented unilaterally compared with when stimuli were presented bilaterally. Further supports come from the studies on split-brain monkeys (Noble,

1966) and monkeys with their optic chiasms cut (Hamilton et al., 1973). Split-brain monkeys learned mirror-image discriminations faster than intact subjects. Monkeys with their optic chiasms cut showed significantly better response when the target and comparison stimuli were presented to the same hemisphere compared with different hemispheres. Thus, avoiding interhemispheric communication by either surgical or behavioral procedures enhances discrimination of mirror-image stimuli. Interestingly, the exception to this rule is split-brain human subjects, who apparently have some difficulty discriminating mirror-image stimuli (Sergent & Corballis, 1989).

It should be pointed out that the baboons studied in this article, the control monkeys studied by Hamilton et al. (1973), and the chimpanzee studied by Matsuzawa (1990) eventually learned to discriminate mirror-image stimuli even though the two cerebral hemispheres could communicate by way of the major callosal fibers. Thus, how did the baboons learn? It might have taken longer for mirror-image discrimination to emerge because inhibition of communication between hemispheres must develop over the training period. Alternatively, the subjects themselves may have imposed an asymmetry in their perception of the stimuli, so as to enhance unilateral presentation. One example of this might be focusing the fovea far away from the stimulus, either left or right, so as to enhance unilateral presentation to or differential rates of information processing for each cerebral hemisphere. This strategy would account for the greater accuracy in intra- versus interhemispheric mirror-image matching found in the control monkeys tested by Hamilton et al. It would furthermore account for the significant mirror-image matching we found in our subjects under conditions of bilateral presentation (see Experiment 3).

This explanation may further account for some of the inconsistent findings reported in pigeons regarding mirror-image discrimination. Pigeons lack binocular vision, and their visual systems are structured such that projection of visual information from one eye is completely contralateral and there are no ipsilateral projections. Thus, looking at the stimuli with one eye is essentially a unilateral presentation. In studies where this is not controlled (i.e., Lohmann et al., 1988), there may be competing engrams in each half of the brain. Under conditions of restricted unilateral input (whether intentional on the part of the experimenter or not), faster learning may emerge. In fact, if this explanation is correct, then animals trained under conditions of unilateral presentation (e.g., presentation to one eye or one hand) should learn significantly faster than subjects trained under bilateral presentation, a hypothesis which remains to be tested.

Some have suggested that experience with stimuli in the three-dimensional domain is necessary to evidence mental rotation when two-dimensional stimuli are presented (Lohmann et al., 1988). We do not agree with this conclusion, for the simple reason that animals have no apparent difficulties in discriminating mirror-image stimuli rotated 180° forward or backward. Mirror-image discrimination problems are almost exclusively limited to the left–right axis (Corballis & Beale, 1976). If problems with mirror-image discriminations were exclusively due to experiences in three
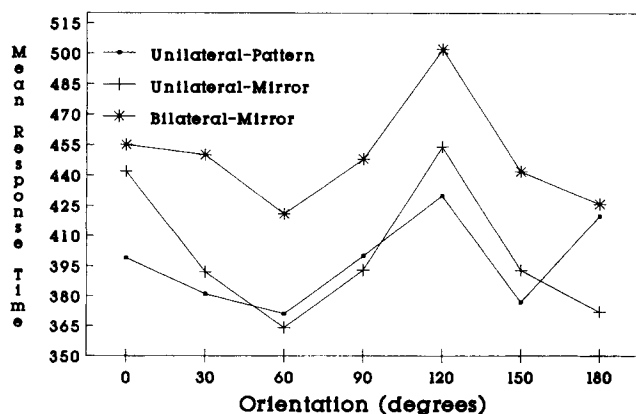

Figure 5. Mean response time at each orientation as a function of presentation input: Unilateral-Pattern (Experiment 2), Unilateral-Mirror (Experiment 2), or Bilateral-Mirror (Experiment 3).

dimensions, then difficulties should be encountered irrespective of the axis of rotation.

It has also been suggested that humans have little difficulty with mirror-image stimuli (and thereby mental rotation) because of functional asymmetries in their brains, such as expressed in handedness (Corballis & Beale, 1976). In other words, according to Corballis (1982), "there is no way, for instance, a bilaterally symmetrical organism can label a letter such as 'R' as distinct from its mirror-image" (p. 192). Assuming that the model proposed by Corballis (1982, 1988) is correct, our subjects could have had functionally asymmetric brains. We, of course, cannot generalize this finding to the species level, but recent evidence clearly suggests that population hand preferences exist in nonhuman primates (Fagot & Vauclair, 1991; MacNeilage et al., 1987). Also, many animals show individual hand preferences (Warren, 1980), and there is no reason that the entire population need be lateralized in the same direction for significant mirror-image discrimination to be observed.

In conclusion, the results from this series of experiments indicate that baboons were able to match mirror-image stimuli and were able to solve a mental rotation task. The baboons, however, solved the mental rotation task in a manner different from that reported in human subjects. On the basis of the extensive literature on identity and conceptual matching in animals (see Roitblat, 1987), we believe that mental rotation can be found in animals, but this affirmation awaits further experimentation. Many variables have not been manipulated, such as speed of stimulus presentation or the number of angular orientations. Still, it is clear that the problem of mirror-image discrimination in animals can be overcome by experimental manipulation. What remains to be determined is how to ask animals to answer the right (or left?) question with respect to their capacity for generating and rotating images.

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