Comparative Assessment of Distance Processing and Hemispheric Specialization in Humans and Baboons (*Papio papio*)

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This comparative study explored the ability to process distance and its lateralization in humans and baboons. Using a conditional matching-to-sample procedure in a divided-field format, subjects had to decide whether or not the distance between a line and a dot belonged to a short- or a long-distance category. Experiments 1, 2, and 4 demonstrated the ability of baboons to process and categorize distances. Moreover, humans showed better distance processing for right visual field/left hemisphere presentations than for left visual field/right hemisphere (LVF-RH) displays (Experiments 1–2). The same bias was found in baboons (Experiment 1), but in a weaker way. In Experiment 3, naive human individuals were tested and the difficulty of the discrimination was enhanced. There was a LVF-RH advantage which vanished with practice. Results are discussed by referring to theories (i.e., Kosslyn, 1987) of visuospatial processing for coordinate and categorical judgments. © 1998 Academic Press

In contrast to the predominant view that the right hemisphere (RH) of humans is superior to the left for all aspects of spatial processing (e.g., Bradshaw & Nettleton, 1981), Kosslyn and his colleagues (e.g., Kosslyn, 1987; Kosslyn, Koenig, Barett, Cave, Tang, & Gabrieli, 1989) argued that both cerebral hemispheres possess spatial abilities. According to these authors, the left cerebral hemisphere (LH) is specialized for categorizing topological relations and the RH is more efficient for computing distances. This theory was supported by empirical evidence (Hellige & Michimata, 1989; Kosslyn et al., 1989; Laeng, 1994; but see Sergent, 1991) and neural network simulations (Kosslyn, Chabris, Marsolek, Jacobs, & Koenig, 1995; Kosslyn,

Chabris, Marsolek, & Koenig, 1992; but see Cook, Früh, & Landis, 1995). In an attempt to identify the underlying mechanisms, Kosslyn (1987) and Kosslyn, Sokolov, and Chen (1989) proposed that cerebral lateralization is founded on an initial LH specialization for language control. However, as recognized by the authors themselves (Kosslyn & Koenig, 1992), hemispheric lateralization also exists in nonhuman species (e.g., Fagot & Vauclair, 1991), though they have no humanlike language abilities. For example, monkeys exhibited an LH advantage for categorizing meaningful auditory stimuli (e.g., Hauser & Andersson, 1997; Heffner & Heffner, 1984; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978). Moreover, an RH advantage was shown in monkeys and in apes in face discrimination tasks (e.g., Hamilton & Vermeire, 1988; Morris & Hopkins, 1993).

The experiments presented in this article were aimed at questioning the evolutionary origins of cerebral specialization for spatial processing in humans. In particular, in line with Kosslyn and collaborators, this research looked for a possible RH advantage in monkeys for tasks that required the processing of distances. Before presenting our studies, we briefly review evidence for (1) distance processing and (2) hemispheric lateralization for visuospatial tasks in animals.

Distance Processing

There are several studies suggesting that animals as different as primates (Czerny & Thomas, 1975; Davis, 1974; Fujita, 1997; McGonigle & Jones, 1978; Menzel, 1973; Thomas & Ingram, 1979; Thomas & Peay, 1976; Wilson, 1972), rodents (Colett, Cartwright, & Smith, 1986), birds (Kamil & Jones, 1997; Pepperberg & Brezinsky, 1991), and insects (Cartwright & Colett, 1983) are capable of perceiving and processing distances, but the literature provides only indirect evidence for this ability. In effect, as these studies were not directly aimed at investigating visual distance processing *per se,* the distance factor was often confounded with other factors. For instance, Thomas and Peay (1976) studied the Piagetian conservation of length in squirrel monkeys (*Saimiri sciureus*). In this study, monkeys were able to perform correct sameness–difference judgments for the lengths of rectangular blocks. However, as recognized by Thomas and Peay (1976), the length factor is confounded with other stimulus dimensions (i.e., area and volume), leaving it uncertain which cue was used by the monkeys to solve the task. More convincing arguments for distance processing in animals are found in a study (Fujita, 1997) showing that the ''Ponzo'' illusion is present in chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*).

Hemispheric Specialization for Visuospatial Tasks

There is now compelling evidence that functional asymmetries related to visuospatial processing do exist in animals (e.g., Fagot & Vauclair, 1991,

1994; Fersen & Gunturkun, 1990; Rogers, 1986), but it remains to be determined if animals and humans exhibit identical forms of lateralization. Indeed, asymmetries reported in the animal literature are sometimes (e.g., global/local processing: Fagot & Deruelle, 1997; face discrimination: Hamilton & Vermeire, 1988), but not always (e.g., line orientation discrimination: Hamilton & Vermeire, 1988), similar to that of humans. There is, to our knowledge, no study on lateralization for distance processing in monkeys or other animals. However, the available database suggests that nonhuman primates are lateralized for topological treatments. Hence, Jason, Cowey, and Weiskrantz (1984) found an LH advantage in rhesus monkeys solving a visual center/off-center discrimination task. Hopkins and Morris (1989) examined visual field asymmetries for processing the relative location (above or below) of a short and a long parallel line in two language-trained chimpanzees (*P. troglodytes*). They found faster reaction times for left than for right visual field presentations.

Four experiments are reported in this article. Their purpose is, first, to demonstrate a baboons' ability to process visual distances and, second, to look for a possible lateralization of this ability. In each experiment, following Hellige and Michimata's (1989) study with humans, baboons had to decide whether the distance between a line and a dot belonged to a short- or a long-distance category. The performances achieved by the baboons are compared to those of human subjects tested with the same procedure, stimuli, and setup. Experiment 1 demonstrates that baboons and humans process distances in a similar way and reveals an LH advantage in humans and one of a more limited extent in baboons. These results are replicated in Experiment 2. Experiment 3 suggests that the LH advantage observed in Experiment 2 rests on an effect of practice, accounting for differences between what would be expected from Kosslyn's theory and our empirical results. Finally, Experiment 4 confirms that baboons processed and categorized distances in Experiments 1 and 2.

EXPERIMENT 1

Method

Subjects. The group of monkeys was composed of six (three males and three females) adult Guinea baboons (*Papio papio*) raised in the animal facilities at the CNRS, Marseille, France. All monkeys were already familiar with the setup and were previously trained on tasks requiring joystick manipulation (e.g., Vauclair & Fagot, 1993), pattern discrimination (Fagot & Vauclair, 1994; Wilde, Vauclair, & Fagot, 1994), rotational invariance problem solving (Hopkins, Fagot, & Vauclair, 1993; Vauclair, Fagot, & Hopkins, 1993), and categorization problems (Dépy, Fagot, & Vauclair, 1997; Fagot, Kruschke, Dépy, & Vauclair, in press; Vauclair & Fagot, 1996). Monkeys were not food deprived during the experiment, but received their daily food ration (monkey chow, fruits, and vegetables) at the end of the day.

The group of human participants was composed of five men and five women who volunteered to participate for pay. Their ages ranged from 23 to 36 years. They reported being

right-handed in each item of a six-item laterality questionnaire (questions asked which hand was used for writing, drawing, ball throwing, tooth brushing, hammering, and using a racket). Subjects also reported having normal or corrected-to-normal vision.

Apparatus. Human and nonhuman primates were tested with the same apparatus. The setup was composed of (1) a 14-inch color computer monitor driven by a PC-AT computer, (2) an analog joystick controlling the movements of a cursor on the monitor, and (3) a touch-sensitive pad (11.5 × 10.0 cm) that served to initiate the trials by the subject placing one hand on it. A software program, written in Turbo Pascal 5.0, controlled the duration of stimulus presentation and the recording of response times at a 1-ms sampling rate.

The monkeys were tested inside an experimental cage (68 × 50 × 72 cm) facing the computer monitor. This cage was fitted with an 8.7 × 8-cm view port which maintained the distance constant (i.e., 48 cm) between the subject's eyes and the screen and two hand ports that could be closed by sliding panels. The testing environment for the baboons also included a food dispenser for delivering 190-mg banana-flavored food pellets inside the cage when correct responses were made.

When humans were tested, they sat at a table on which a monitor was placed at eye level. The viewing distance from the screen was controlled with a vertical cartonboard in which an 8.7 × 8-cm view port and two hand ports were cut. This board was attached to the front side of the table.

General procedure. The same testing procedure was adopted for the two species. It consisted of a conditional matching-to-sample task in which the sample form was briefly displayed in either the left visual field (LVF) or in the right visual field (RVF). The subject initiated the trials by placing one hand on the touch pad. Immediately afterward, a green cursor (0.5 cm in diameter) appeared in the center of the screen along with a white .5 × .5-cm square-shaped fixation stimulus (F.S.), which was displayed either 1.5 cm above or below the cursor. In response to this display, the subject was required to manipulate the joystick so as to place the cursor for 35 ms on the fixation stimulus. Wilde, Vauclair, and Fagot (1994) demonstrated that this behavioral constraint imposed a fixation of the gaze on the F.S.

Once the cursor was maintained on the F.S., a sample stimulus appeared during 120 ms in the left or the right hemiscreen. The inner edge of the sample stimulus was laterally displaced from the F.S. by 3 degrees of visual angle. Hence, the sample stimulus was presented in one visual half-field at a time because it was shown for a duration shorter than the time required to perform goal-directed saccadic eye movements (Wilde et al., 1994) and at a retinal eccentricity that ensured a contralateral projection of the visual input (Leventhal, Ault, & Vitek, 1988).

Immediately after the lateralized presentation of the sample stimulus, the trial continued with the simultaneous display of a red and a green 3 × 3-cm response stimulus. The red response stimulus was shown 4 cm above the center of the screen and the green one appeared 4 cm below the center. On an arbitrary (experimenter-defined) basis, the subject was then required to manipulate the joystick so as to touch with the cursor the response stimulus matching the sample. A correct response was recorded if the subject chose the response associated to the sample. In all the phases of this study (training and testing), correct responses were accompanied by a tone and, for baboons, by the additional delivery of a food pellet. For the two species, incorrect responses were followed by a low raucous tone and a time-out ranging from 2 to 5 s.

Stimuli. Twenty yellow sample stimuli were presented during the test. They were all shown on a black background. Each stimulus consisted of a 3 × .2-cm horizontal line fitted with a dot (.5 cm in diameter). For 10 stimuli, the dot was located above the line (see Fig. 1). For the remaining 10, it was below the line. For each dot location, the distance between the dot and the line could be .1, .3, .5, .7, .9, 1.9, 2.1, 2.3, 2.5, or 2.7 cm. Stimuli could thus be classified as belonging to a short- (range, .1–.9 cm) or a long-distance category (range, 1.9–2.7 cm). One important feature of these stimuli is that they differed by one dimension only; that is, the distance between the line and the dot. In particular, they were all isoluminant, preventing subjects to rely on luminance discrimination for responding. Furthermore, the sample stimuli could appear equally often 1 cm above, 1 cm below, or at the same horizontal
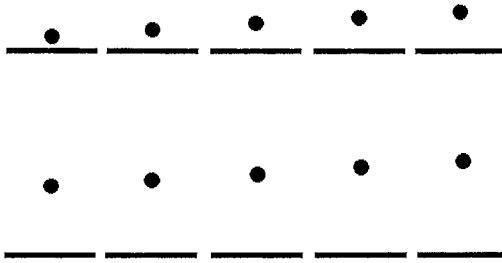
FIG. 1. Stimuli of the short- (top) and long-distance categories (bottom) used in Experiment 1. Stimuli in which the dot was below the line are not represented here.

level as the F.S., ruling out the possibility of using the absolute location of the dot to respond correctly.

Training. The training phase was designed to have subjects of each species learn the matching rule. Four training stimuli were used. They were made by combining two line–dot distances (.1 or 2.7 cm) and two dot locations (above or below the horizontal line). Half of the subjects from each species were requested to select the red square-shaped response stimulus when .1 cm separated the dot from the line or the green one when the line–dot distance was equal to 2.7 cm. For the other half, the matching rule was reversed. In order to avoid procedural differences between the two species, human subjects were never told what the matching rule was, but had to discover it for themselves. For each species, training continued until a training criterion of 80% correct over a series of 80 trials was met. On average, 1345 trials (range, 854–2217 trials) were needed for the baboons to meet the training criterion. Humans learned the task more rapidly than baboons (less than 100 trials each). For each subject, either a human or nonhuman primate, the use of left and right hand during training was balanced.

Testing. Humans performed at a high level on this task. Thus, they received less testing trials than monkeys in order to avoid ceiling effects. The experiment involved eight sessions of 120 trials each ($N = 960$) for the baboons and two sessions of 120 trials each ($N = 240$) for humans. Half of the sessions for each species involved the use of the left hand for joystick manipulation. The remaining half involved right-hand manipulations. Within a session, each stimulus served six times as the sample, three times in each visual field. The order of sample stimulus presentation was pseudo-random, with the constraint that no more than three consecutive trials implied stimulus presentation in the same (left or right) visual half-field.

Results

Scores. A first analysis of variance (ANOVA) verified the effect of species (humans, baboons), visual field (left, right), and line–dot distance (.1, .3, .5, .7, .9, 1.9, 2.1, 2.3, 2.5, and 2.7 cm) on arcsine-transformed score data. The hand factor was not retained for analysis because preliminary analyses showed that this factor never interacted significantly with the visual half-field factor (all ps $> .10$). The three-way ANOVA revealed a complex pattern of results. First, the main effect of species was significant, $F(1, 14) = 99.17$, $p < .001$. On average, humans scored better than baboons ($M = 90.4$ and 74.9%, respectively). Second, the main effect of distance was significant, $F(9, 126) = 17.15$, $p < .001$. The distance factor, however, was involved in a significant species-by-distance-by-visual field interaction, $F(9, 126) = 2.3$, $p < .02$. In order to understand this three-way interaction, follow-up
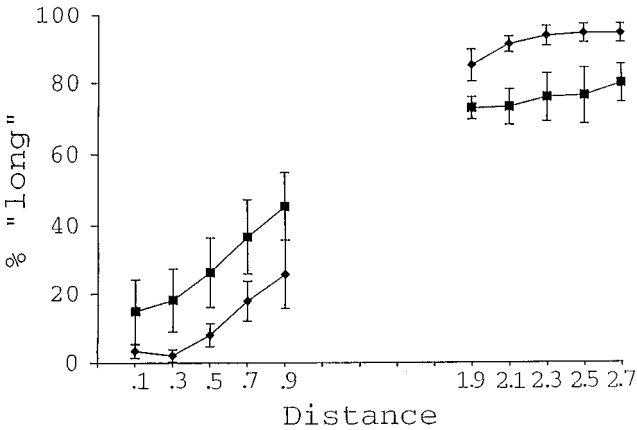
FIG. 2.   In Experiment 1, percentage of long responses and confidence intervals at $p = .05$ for each species (diamond, humans; square, baboons) and line–dot distance (in centimeters).

analyses involving the visual half-field (LVF, RVF) and the line–dot distance (.1, .3, .5, .7, .9, 1.9, 2.1, 2.3, 2.5, and 2.7 cm) were conducted for each species independently.

The average performance for the baboons was equal to 74.9% correct (range, 65.2–85%). Based on the computation of a two-tailed χ^2 test ($p < .05$), all monkeys performed significantly above chance. The field-by-distance ANOVA on the baboon's data demonstrated the main effect of distance as significant, $F(9, 45) = 7.05, p < .001$. This effect showed that the percentage of ''long'' responses increased with the line–dot distance (see Fig. 2). The ANOVA on scores also revealed a significant field-by-distance interaction, $F(9, 45) = 2.67, p < .02$, showing a significant (Duncan, $p < .05$) RVF-LH score advantage for the distances of .7 and .9 cm, but not for the other distances (see Table 1).

The data from humans are very similar to those of the baboons (see Fig. 2), although humans performed higher on average ($M = 90.4\%$; range, 88.7–93.3%) than monkeys. The field-by-distance ANOVA revealed a significant main effect of distance, $F(9, 81) = 11.05, p < .001$. On the basis of Duncan post hoc comparisons ($p < .05$), scores were lower for the distances of .7 and .9 cm than for the more extreme distances. The field-by-distance interaction was also significant, $F(9, 81) = 2.9, p < .005$, and demonstrated significant (Duncan test, $p < .05$) RVF-LH advantage for .5 cm, but no significant field differences for the other distances.

Response times. Response times were defined as the time elapsed between the offset of the sample stimulus and the detection of a collision between the cursor and one of the two response stimuli. The analysis of response times followed the same logic as for scores. Thus, for each species, response

TABLE 1
Mean Accuracy as a Function of Species, Line–Dot Distance
(in cm) and Visual Field in Experiment 1

Distance	Baboons		Humans	
	LVF	RVF	LVF	RVF
.1	84.0	86.4	97.5	95.8
.3	79.0	84.9	100	95.8
.5	68.9	78.6	87.4	96.7
.7	54.8	71.9	81.7	82.5
.9	48.5	60.4	73.6	75.0
1.9	75.6	70.6	86.7	84.2
2.1	75.7	71.2	90.8	92.5
2.3	80.2	72.3	92.5	95.8
2.5	74.3	79.1	97.5	92.5
2.7	80.5	80.0	97.5	92.5

times for correct trials were subjected to a field (RVF, LVF)-by-line–dot distance (.1–2.7 cm) ANOVA.

Baboons' response times averaged to 631 ms (range, 207–1179 ms). The analysis of correct response times revealed no significant main effect or interaction. Considering human participants, average response time was 417 ms (range, 247–615 ms). Two main effects emerged from the field-by-distance ANOVA. First, the effect of distance was significant, $F(9, 81) = 6.62$, $p < .001$. For the distances of .7 and .9 cm, response times were slower on average (Duncan test, $p < .05$) than for the extreme distances. Second, the main effect of visual field was significant, $F(1, 9) = 6.75$, $p < .05$. Humans responded faster on average when the sample was presented in RVF-LH ($M = 415$ ms) than when it was presented in LVF-RH ($M = 426$ ms).

Discussion

At least two conclusions may be derived from Experiment 1. First, considering that the unique cue in solving the task was the distance between the line and the dot, for both humans and baboons, distance processing is demonstrated through the systematic variations in the percentages of the ''long'' responses as a function of the line–dot distance. Second, humans showed an RVF-LH advantage in response times. Lateralization in humans is not derived from a speed–accuracy trade-off because laterality effects were not found for scores. Monkeys also showed a score advantage for RVF-LH presentations, but field asymmetries for scores were significant for the distances of .7 and .9 cm only.

EXPERIMENT 2

The observation of an LH advantage in our human subjects contradicts previous findings of a primary RH involvement for distance processing (e.g.,

Kosslyn et al., 1989). Before concluding on this discrepancy, we wanted to assess the reliability of our results in a second experiment. Thus, Experiment 2 retested the same subjects as in Experiment 1, but with a slightly different procedure. In Experiment 2, the gap separating the two categories was reduced from 1 cm to .4 cm. It was expected that this manipulation would enhance the difficulty of the task, giving a greater emphasis on the ability of the subjects to discriminate the long from the short distances.

Method

Subjects, apparatus, and stimuli. Experiment 2 used the same subjects and apparatus as in Experiment 1. Testing stimuli were similar to those of Experiment 1, but the line–dot distances were set at .4, .6, .8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.2, or 2.4 cm.

Testing procedure. For baboons, about 2 weeks elapsed between Experiments 1 and 2. Therefore, baboons were retrained with the four training stimuli of Experiment 1 until they met a criterion of 80 correct responses over 100 consecutive trials. Less than 120 trials were needed on average to reach the criterion. Humans were not retrained, because Experiment 2 was proposed to them immediately after Experiment 1.

During testing, the baboons performed eight sessions of 132 trials each. Humans were presented with two sessions only. Within a session, each stimulus ($N = 22$) was displayed three times in each visual half-field. On every trial, correct responses were indicated by delivering a food pellet and a tone to baboons and only a tone to humans. Because 1.4 cm was exactly in between the two extreme distances, trials with these 1.4-cm stimuli were randomly reinforced using a 50% reinforcement schedule. Other experimental constraints (for instance, handedness, controlled cues, nature of response stimuli, or matching rule) were identical to those of Experiment 1.

Results

The data set was analyzed following the same procedure as in Experiment 1. Moreover, given that the trials with a line–dot distance of 1.4 cm followed a different reinforcement schedule than the other stimuli, these trials were discarded from the analyses.

Scores. Computation of two-tailed χ^2 tests ($p < .05$) demonstrated that each monkey performed significantly above chance (range, 63.5–79.5%). The field-by-distance ANOVA revealed distance as the only significant effect, $F(9, 45) = 6.79$, $p < .001$. Performances were lower for the intermediate distances (1.2, 1.6, and 1.8 cm) than for .4 cm (see Fig. 3 and Table 2).

On average, human subjects reached an accuracy score of 84.8% (range, 78.3–88.8%). The field-by-distance ANOVA showed that the effect of distance, $F(9, 81) = 23.87$, $p < .001$, and the field-by-distance interaction, $F(9, 81) = 2.19$, $p < .01$, were both significant. Regarding the effect of distance (see Fig. 3), the 1.2-, 1.6-, 1.8-, and 2-cm distances gave rise to lower performances than all the other distances (Duncan, $p < .05$). Regarding the interaction, post hoc analyses (Duncan test, $p < .05$) showed an advantage for RVF-LH compared to LVF-RH presentations for 1.2 cm and a reversed effect for 1.6 cm (see Table 2).
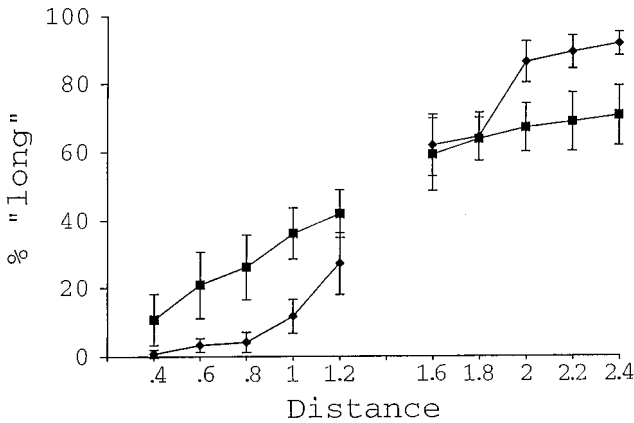
FIG. 3. In Experiment 2, percentage of long responses and confidence intervals at $p = .05$ for each species (diamond, humans; square, baboons) and line–dot distance (in centimeters).

Response times. On average, baboons responded in 642 ms (range, 295–1154 ms). Computation of a field-by-distance ANOVA failed to show any significant main effect or interaction.

On average, human participants needed 424 ms (range, 247–615 ms) to respond. The ANOVA revealed a significant effect of distance, $F(9, 81) = 7.13$, $p < .001$, and a significant field-by-distance interaction, $F(9, 81) = 2.11$, $p < .05$. Humans responded slower (Duncan test, $p < .05$) to the 1.8-cm distance than to shorter and longer distances. The interaction indicated faster RVF-LH responses ($M = 479$ ms) compared to LVF-RH responses ($M = 628$ ms; Duncan test, $p < .05$) when the 1.8-cm distance was used. No other field differences were significant for the remaining distances.

TABLE 2
Mean Accuracy as a Function of Species, Line–Dot Distance
(in cm) and Visual Field in Experiment 2

Distance	Baboons		Humans	
	LVF	RVF	LVF	RVF
.4	84.5	94.0	98.3	100
.6	73.5	84.7	96.7	96.7
.8	65.0	82.8	95.8	95.8
1.0	54.8	73.0	90.8	95.8
1.2	48.5	67.5	79.2	66.5
1.6	70.2	49.1	63.3	66.7
1.8	72.2	55.3	51.7	74.2
2.0	75.0	59.53	83.3	89.9
2.2	75.6	62.5	86.7	92.5
2.4	77.1	64.6	90.8	93.3

Discussion

The aim of Experiment 2 was to evaluate the reliability of the findings of Experiment 1. In this respect, the resemblance between Figs. 2 and 3 is striking and confirms previous conclusions on the use of the line–dot distances for responding.

Altogether, Experiments 1 and 2 provided only weak evidence for hemispheric specialization, as the RVF-LH advantage observed for humans (Experiment 1) was restricted to response times and was not replicated in Experiment 2 (except for 1.8 cm). These findings contradict previously reported evidence for an RH specialization for distance processing in humans (e.g., Hellige & Michimata, 1989; Kosslyn et al., 1989; Rybash & Hoyer, 1992). It should be noted, however, that the observed RH advantages reported in the literature were mostly apparent in early trials and frequently vanished after repeated testing (e.g., Kosslyn et al., 1989). According to Kosslyn (1994), the effect of practice may be explained by a progressive involvement of the LH for categorization, eliminating the RH advantage for distance processing.

In order to investigate if an RH advantage was present early in testing, the first testing session of Experiment 1, for which subjects were naive, was retained for a complementary field-by-distance ANOVA. Regarding scores, there was no main effect of field for either baboons or humans. For response times, the effect of field was not significant for the baboons, but it was significant for humans and still showed an RVF-LH advantage, $F(1, 9) = 5.9$, $p < .05$. Therefore, data on the first session provided no evidence for an RH advantage for distance processing.

It might be argued that the ''long'' and ''short'' categories of Experiment 1 were easily distinguishable (1 cm separated them) which might have favored a categorical treatment of the task. In Experiment 2, discrimination was more difficult but hemispheric biases might have been masked by a practice effect as the subjects were no more naive. In Experiment 3, a sample of novel human subjects was thus tested in the same conditions as in Experiment 2. An RH advantage was expected in the early trials of this experiment.

EXPERIMENT 3

Method

Subjects (five men and five women) were selected on the same criteria as in Experiment 1. The apparatus, stimuli, and testing procedure were similar to those of Experiment 2 except that participants received the same training as the human participants in Experiment 1.

Results

On average, subjects reached an accuracy score of 86.1% (range, 82.9–90.4%). Arcsine-transformed score data were submitted to a distance (.4, .6,

TABLE 3
Mean Accuracy as a Function of Line–Dot Distance (in cm), Session,
and Visual Field in Experiment 3

	LVF		RVF	
Distance	Session 1	Session 2	Session 1	Session 2
.4	100	100	98.3	100
.6	100	96.7	91.7	100
.8	98.9	100	88.3	100
1.0	85.0	90.0	75.0	91.7
1.2	63.0	70.0	63.3	80.0
1.6	78.3	71.7	68.3	66.7
1.8	71.7	66.7	55.0	65.0
2.0	93.3	91.7	81.7	81.7
2.2	90.0	96.7	91.7	93.3
2.4	100	98.3	100	93.3

.8, 1.0, 1.2, 1.6, 1.8, 2.0, 2.2, and 2.4 cm)-by-testing session (1, 2)-by visual field (LVF, RVF) ANOVA. The main effect of distance was significant, $F(9, 81) = 33.61$, $p < .001$, and showed lower performances for the intermediate distances than for the extreme ones. The main effect of session was also significant, $F(1, 9) = 11.25$, $p < .01$. This effect demonstrated greater scores on average in the second session ($M = 84.7\%$) than in the first one ($M = 80.8\%$). There was also a significant session-by-visual field interaction, $F(1, 9) = 14.15$, $p < .005$, showing a significant (Duncan test, $p < .05$) LVF-RH advantage in the first session (M RVF = 79.9%; M LVF = 83.8%) but no field difference in the second session (M RVF = 84.4%; M LVF = 85.2%). Of particular interest, performances for RVF-LH trials improved (Duncan test, $p < .05$) from session 1 to session 2, whereas performances for LVF-RH trials remained constant, suggesting that only the LH benefited from practice (see Table 3). Finally, the session-by-distance interaction was significant, $F(9, 81) = 2.15$, $p < .05$. This interaction showed an improved performance with practice for 1.2 cm, but no practice effects for the other distances.

Considering response times ($M = 544$ ms; range, 318–759 ms), the field-by-distance-by-session ANOVA revealed a significant effect of distance, $F(1, 9) = 27.7$, $p < .01$. Participants responded slower (Duncan test, $p < .05$) to 1.2, 1.6, and 1.8 cm than to the smaller and larger distances. The main effect of session was significant, $F(9, 81) = 6.6$, $p < .001$, and revealed shorter response times in session 2 ($M = 470$ ms) than in session 1 ($M = 613$ ms). Other main effects or interactions never reached significance.

Discussion

Scores of Experiment 3 demonstrate an LVF-RH advantage in the early trials of the distance discrimination task. This result shows the reality of the

RH advantage suggested by Kosslyn (1987) for distance processing in humans. Comparison of the findings from Experiments 1–3 shows, moreover, that this effect is fragile. It is affected by the familiarity of the subjects with the task and by the task demand.

EXPERIMENT 4

This experiment was aimed at assessing whether baboons' performances could rely on a mechanism of generalization or on categorical processes. This question is derived from inspection of Figs. 2 and 3. At this point, the performance decrement observed for intermediate distances (see Figs. 2 and 3) may be interpreted in two different ways. First, it can be argued that this effect reflects the difficulty in assigning these borderline stimuli to one of the two categories. Second, this effect may also be accounted for by a process of stimulus generalization because the weakest scores were associated to the maximal perceptive differences between the test and training stimuli. Ruling out the stimulus generalization hypothesis was important for our purpose, since stimulus generalization implies an inability to discriminate stimuli on a categorical basis (Thomas, 1996; Thomas & Lorden, 1993; but see Shepard, 1987).

In order to test the hypothesis of stimulus generalization, an additional transfer test was administered to the baboons. In this experiment, monkeys were presented with novel long distances (i.e., 2.9, 3.1, 3.3, 3.5, and 3.7 cm) intermixed with the short and long distances used in Experiment 1. If generalization occurred, then performance levels were expected to decrease from 2.7 to 3.7 cm due to the increasing physical difference between training and test stimuli. By contrast, if performance levels relied on categorical processes, then they should remain constant for all long distances despite the physical disparity between the test and training stimuli.

Method

The same baboons as in the previous experiments were tested except one, a female, who accidentally died for a reason unrelated to the experiment. The stimuli and testing procedures were identical to those in Experiment 1 except that five novel long distances (i.e., 2.9, 3.1, 3.3, 3.5, and 3.7 cm) were added to the stimulus set. About 1 year elapsed between Experiment 2 and this experiment. Prior to testing, baboons were thus retrained using the same training stimuli as in Experiment 1. On average, they needed 1017 trials (range, 342–2082 trials) to reach the training criterion of 80 correct responses over 100 trials.

During testing, each baboon performed four sessions of 180 trials. Within a session, each stimulus ($N = 30$) was displayed three times in each visual half-field. The other procedural aspects of the task were identical to those of Experiments 1 and 2.

Results

Subjects reached an average accuracy score of 81.4% (range, 73.2–87.9%). Mean response time was equal to 797 ms (range, 342–1372 ms).
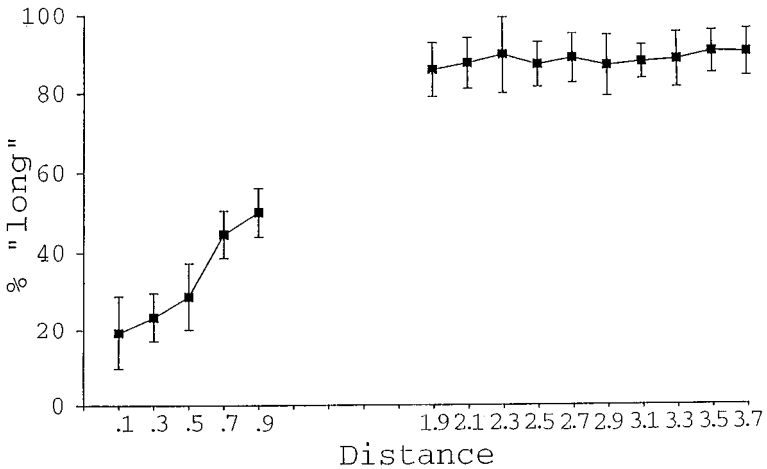
FIG. 4. In Experiment 4, percentage of long responses and confidence intervals at $p = .05$ for each line–dot distance (in centimeters).

Because no significant effects were found for response times, score data only are presented. As in the previous experiments, score data were first submitted to an arcsine transformation and then subjected to a field (LVF, RVF)-by-distance (.1, .3, .5, .7, .9, 1.9, 2.1, 2.3, 2.5, 2.7, 2.9, 3.1, 3.3, 3.5, and 3.7 cm) ANOVA. Only the main effect of distance was significant, $F(14, 56) = 15.76$, $p < .001$. As shown in Fig. 4, scores were lower (Duncan test, $p < .05$) for the .7- and .9-cm distances than for the other more extreme distances. Note that there was no significant difference between any of the 10 long distances, which is not compatible with the stimulus generalization hypothesis.

Remember, however, that the data points shown in Fig. 4 result from averaging 48 trials for each point. Because learning may have occurred in 48 trials, we verified how baboons responded at the very first presentations of the five novel distances. Data on these trials are reported in Table 4. As shown in Table 4, one baboon was correct for three of the five initial presentations, two other baboons were correct four of five times, and the remaining two were systematically correct whatever the distance. Altogether, the inspection of the first trials suggests an immediate and positive transfer with novel distances rather than the learning of novel stimulus–response associations.

GENERAL DISCUSSION

The present research investigated distance processing and its lateralization in a comparative perspective by using identical stimuli and similar testing procedures with humans and baboons.

TABLE 4
Trial 1 Responses to the Novel Line–Dot Distance (in cm) Presented
in Experiment 4

Subjects	Distances[a]					Total
	2.9	3.1	3.3	3.5	3.7	
B03	0	1	1	1	0	3
B06	1	1	1	0	1	4
B07	1	1	0	1	1	4
B08	1	1	1	1	1	5
B09	1	1	1	1	1	5
Total	4	5	4	4	4	21

[a] 1 = correct choice; 0 = erroneous choice.

Results demonstrated that nonhuman primates (i.e., baboons) processed visual distances and that these animals compared well to humans in this capacity. Distance processing is demonstrated by lower performance for the intermediate distances than for the extreme distances (see Experiments 1 and 2). Interestingly, not only did baboons prove capable of processing distances, but they also showed the ability to apply a categorical treatment to them, as demonstrated by a positive and immediate transfer of performance with novel distances (see Experiment 4). There are several reports of evidence that nonhuman primates are able to categorize visual stimuli (e.g., Dépy, Fagot, & Vauclair, 1997; Schrier, Angarella, & Povar, 1984; Vauclair & Fagot, 1996). In accordance with previous reports of perceptual categorization using a stimulus dimension that varied along a continuum (e.g., for the perception of visual materials in humans: Beale & Keil, 1995; Etcoff & Magee, 1992; for the perception of acoustical material in nonhuman primates: Snowdon, 1990), our experiments demonstrate the baboons' ability to categorize stimuli whose distances varied along a continuum.

In a different perspective, several papers also provided indirect evidence for distance processing in nonhuman primates (e.g., Thomas & Peay, 1976). An important finding of the current research is that monkeys may both process and categorize distances in a task for which the distance is the unique relevant cue.

Another objective of this research was to study lateralization. At the origin of our experimental design, there was the hypothesis that humans process distances more efficiently with their RH than with their LH (e.g., Hellige & Michimata, 1989; Kosslyn et al., 1989). The current research provides mixed support for this conclusion. First, Experiments 1 and 2 demonstrated an LH instead of an RH advantage in humans and one of a limited extent in baboons. Second, an RH advantage appeared with naive human subjects in Experiment 3, but this effect was restricted to early trials. It could be argued that some procedural variations between our research and previous ones might explain

these differences between studies. For example, the vertical eccentricity of the sample stimulus varied accross trials in our research, while it remained constant in previous studies with humans (e.g., Kosslyn et al., 1989). Although it cannot be ruled out that such procedural variations might account for some of the results (for a discussion of procedural effects, see Bruyer, Scailquin, & Coibion, 1997), we favor an explanation based on a practice effect that could have masked the expected RH advantage.

In Experiment 1, the long- and short-distance categories were easily distinguishable, because 1 cm separated them. In Experiment 2, the task was made more difficult (only 0.4 cm separated the two categories), but the subjects were the same as in Experiment 1. It is only in Experiment 3, for which subjects were naive and categorization was made difficult, that an RH advantage emerged. Kosslyn (1987) advocated a specialization of the RH for distance processing in conjunction with a specialization of the LH for categorization. The current results are congruent with this hypothesis. They demonstrate, however, that the RH advantage for distance processing is not persistent and may easily be masked by practice effects recruiting categorical abilities for which the LH excels (see Kosslyn, 1994, pp. 202–203). Recently, Bruyer et al. (1997) showed that the LH vs RH dissociation for categorical vs coordinate computations proposed by Kosslyn (1987) is sensitive to methodological factors such as the subjects' age, the mode of response (vocal vs manual), the feedback (present vs absent), and the type of response (''binary'' vs ''continuous'' response), thus suggesting some limits for this theory.

Turning now to baboons' lateralization, these animals never presented an RH advantage in our tasks. However, they presented some evidence (1) for an LH advantage in Experiment 1 and (2) for the use of categorical strategies (see Experiment 4). As for humans, the ephemeral RH advantage in distance processing might have been hidden by practice effects favoring an LH bias. Indeed, the large number of training trials might have facilitated categorical procedures for which the LH appears to be predominant. While the present data increase the existing body of evidence for hemispheric specialization in nonhuman primates (see for recent reviews: Bradshaw & Rogers, 1993; Fagot & Vauclair, 1991; Hellige, 1993), it remains to be specifically addressed if the LH bias we observed in the present study reflects categorical strategies in baboons. Finally, the results of the present experiments suggest that cerebral specialization for the processing of spatial relations has a long evolutionary history. This view is in agreement with the observation that the laterality for spatial processing in humans is independent of laterality for speech processing (e.g., Boles, 1992; Hellige, 1997).

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