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Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*)

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Abstract

This study was designed to examine whether chimpanzees and monkeys exhibit a global-to-local precedence in the processing of hierarchically organized compound stimuli, as has been reported for humans. Subjects were tested using a sequential matching-to-sample paradigm using stimuli that differed on the basis of their global configuration or local elements, or on both perceptual attributes. Although both species were able to discriminate stimuli on the basis of their global configuration or local elements, the chimpanzees exhibited a global-to-local processing strategy, whereas the rhesus monkeys exhibited a local-to-global processing strategy. The results suggest that perceptual and attentional mechanisms underlying information-processing strategies may account for differences in learning by primates.

Keywords

Visual perception; Global–local processing; Chimpanzees; Monkeys; Gestalt perception

Introduction

Experimental investigation into the abilities of nonhuman animals to perceive and categorize complex stimuli has enjoyed a long history in comparative psychology (see reviews by Roitblat 1987; Wasserman 1993). In the current study, we addressed a very basic question. How difficult is it for chimpanzees and monkeys to discriminate stimulus patterns that differ on the basis of their local elements, global configuration, or both? Our interest in this comparative question is derived, in part, from animal learning studies as well as studies of human perception and selective attention.

Specifically, several investigators have examined the role of attention and memory in the processing of perceptual elements that comprise compound stimuli (Maki and Leuin 1972; Cox and D'Amato 1982; Riley 1984; Lamb 1988, 1991). For example, in a matching-to-sample paradigm, a red circle with a white horizontal line is presented as the sample stimulus.

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Subsequently, two comparison stimuli are presented; the positive comparison stimulus is the one that contains one relevant and overlapping characteristic derived from the sample stimulus (e.g., a white horizontal line or a red square) whereas the foil is a stimulus that has no perceptual overlap with the sample stimulus. These types of trials are compared with performance on trials in which the sample stimulus is derived from only one perceptual element such as color or shape. Results indicate that pigeons and monkeys perform significantly better on trials in which the stimuli are derived of a single perceptual element compared to compound stimulus trials. There remains some debate over the interpretation of these results, with some suggesting that the poorer performance on the compound test trials is due to stimulus generalization decrements (Cox and D'Amato 1982; D'Amato and Salmon 1984; Grant and MacDonald 1986) while others have suggested that there is a "limited capacity" for the amount of information that can be encoded within a given time frame by pigeons and monkeys (Riley and Roitblat 1978).

The research on visual perception and attention in animals has typically employed stimuli that differ on the perceptual dimensions of shape and color. Moreover, most of these studies have used pigeons as subjects. These studies have been very important in elucidating basic mechanisms involved in visual processes but there are limitations in the use of pigeons as subjects. For example, the visual system of pigeons (as in many birds) is organized differently from that of primates in that all visual pathways from the eye to the brain project contralaterally. In contrast, primates have both ipsilateral and contralateral pathways to the brain from each eye. This basic difference could have pronounced effects on how pigeons and primates perceive and attend to different aspects of visual stimuli. Thus, from a comparative perspective, examining aspects of visual perception in nonhuman primates seems warranted on both theoretical and empirical grounds.

In the present study, we examined whether nonhuman primates differentially process compound stimuli that differ on the basis of their global configuration compared to their local elements. Specifically, we were interested in determining whether there is hierarchical processing in the perception of complex stimuli. Studies of perception and selective attention in human subjects suggest that there is a global-to-local precedence in the processing of complex stimuli (Kimchi 1992). Human subjects respond significantly more slowly and with less accuracy when discriminating stimuli on the basis of their local elements compared to their global configuration (Navon 1977). For example, identifying the larger letter "F" constructed of smaller letter "Es" takes longer when asked to identify the local elements rather than the global configuration of the stimulus (herein referred to as the global/local paradigm). Thus, at one level, we were interested in testing whether monkeys and chimpanzees selectively attend to certain aspects of complex stimuli that are less perceptually prevalent than the dimensions of color and shape. Previous studies in baboons and chimpanzees suggest that species differences may exist. For example, Fagot and colleagues (Deruelle and Fagot 1997; Fagot and Deruelle 1997; Fagot and Tomonaga 1999) reported that baboons show local-to-global precedence in processing compound stimuli whereas chimpanzees show no precedence in hierarchical processing of compound stimuli. In contrast, Hopkins (1997) reported a global-to-local precedence in processing compound stimuli. These results are consistent with the study by Fujita and Matsuzawa (1988), who reported that the chimpanzee Ai typically identified outer features of geometric symbols first compared to inner features.

One limitation in comparing the existing findings between monkeys and apes is that different species have not necessarily been tested using the same stimuli and testing procedures. In addition, some studies in chimpanzees have used very small sample sizes in comparison to sample sizes used with Old World monkeys. The purpose of this study was to assess hierarchical processing of compound stimuli in a sample of rhesus monkeys and chimpanzees using the same stimuli and procedures. If nonhuman primates exhibit global-to-local precedence in the processing of compound stimuli then performance should be better for stimuli

that differ on the basis of their global configuration compared to stimuli that differ in their local elements.

Methods

Subjects

Five juvenile chimpanzees (*Pan troglodytes*), three males (Scott, Lamar, and Jarred) and two females (Dara and Katrina), ranging in age from 5 to 6 years, served as subjects. Four of the chimpanzees were raised in the Yerkes Regional Primate Research Center nursery following standard nursery protocol for great apes (see K.A. Bard 1996, Responsive care: behavioral intervention for nursery-reared chimpanzees. Available from Jane Goodall Institute, Ridgefield, CT 06877 USA), whereas Dara was raised by her biological mother at this same facility. Five captive-born male rhesus monkeys (*Macaca mulatta*) were subjects. The rhesus monkeys ranged in age from 3.5 to 14 years of age and were tested at Georgia State University's Sonny Carter Life Sciences Laboratory. All subjects were skilled in the use of the joystick test system prior to this study and could perform the simultaneous and sequential matching tasks employed here (Rumbaugh et al. 1989; Washburn et al. 1989; Hopkins et al. 1996). However, the stimuli used in the present study were novel to all subjects.

Apparatus

Subjects were tested with computerized test systems, described in detail elsewhere (e.g., Rumbaugh et al. 1989; Washburn and Rumbaugh 1992). Each test system consisted of a personal computer (386 compatible), a 13-inch color monitor, and an analog joystick. For the rhesus monkeys, a Gerbrands 5150 pellet dispenser was used for delivery of 97-mg fruit-flavored pellets (Noyes, Lancaster, N.H., USA). Food reinforcement for the chimpanzees was hand delivered by the experimenter.

Stimuli

Hierarchically structured stimuli (large patterns constructed of smaller elements of the same patterns) were used during training and testing. These stimuli, depicted in Fig. 1, measured 3.5 cm high by 2.5 cm wide and were in white presented on the black background of the computer monitor. Each small element that made up the large stimulus was 7×7 mm in dimension and was separated by 1 mm from each adjacent element. For all three stimulus sets, combinations of the sample and comparison stimuli required that subjects differentiate the stimuli on the basis of either their local elements, global configuration, or both (LOCAL, GLOBAL, or BOTH conditions, respectively). In Fig. 1, for all three stimulus sets, stimulus pairs 1 and 3 and 2 and 4 differ on the basis of local elements. Stimulus pairs 1 and 2 and 3 and 4 differ in their global configuration. Stimulus pairs 1 and 4 and 2 and 3 differ on the basis of both their global configuration and local elements.

Procedure

Training—Because the stimuli and discrimination problems were novel to the subjects, some training on the discriminations to be performed in this experiment were performed prior to the tests for hierarchical processing. Subjects were tested in their home cages on a simultaneous matching-to-sample (MTS) task. Each MTS trial began when a sample stimulus, randomly selected from libraries of stimuli 1 and 2 depicted in Fig. 1, appeared in the center of the computer monitor. The cursor (a white plus sign measuring approximately 1.25×1.25 cm) was positioned 5 cm below the sample stimulus. Subjects were required to manipulate the joystick so as to direct a collision between their cursor and the sample stimulus, whereupon two comparison stimuli were presented. The positive comparison stimulus was identical to the sample; the foil stimulus was a nonmatching stimulus randomly selected from the library. The

comparison stimuli were presented in random position 5 cm to the left and right of the sample stimulus. A correct response was recorded when the subjects directed a collision between their cursor and the identical comparison stimulus and was followed by the delivery of food reinforcement and a high-pitched tone. Incorrect responses were recorded when the subjects directed a collision between their cursor and the foil stimulus and resulted in a low, raucous tone and no delivery of food reinforcement.

On any trial, the foil could differ from the sample in its global configuration, its local elements, or both. These were considered to be the three different types of concurrent MTS problems, GLOBAL, LOCAL and BOTH, respectively. Thus, the presentation of different types of MTS problems was randomly determined within a test session. The order of administration of the two stimulus libraries was arbitrary across animals (i.e., three chimpanzees and three monkeys were initially trained with stimulus set 1, whereas the remaining animals were first trained with stimulus set 2).

Each subject was trained until 50 consecutive trials for each problem type were completed with a matching accuracy in excess of 70%. Once subjects had attained criterion on GLOBAL, LOCAL, and BOTH problems, a generalization test was conducted using the second stimulus set. Subjects trained on stimulus set 1 were tested for generalization using stimulus set 2, whereas subjects trained on stimulus set 2 were tested for generalization with stimulus set 1. During the generalization test, each subject received 50 GLOBAL, LOCAL, and BOTH test trials in random order. Percent correct as a function of the type of problem was the dependent measure for the generalization test.¹

Testing—For testing, a sequential, rather than simultaneous, matching-to-sample paradigm was employed because we wanted to control the exact amount of time subjects' could attend to the sample stimulus (described in detail by Hopkins et al. 1990; Hopkins 1997). All subjects had been trained on the sequential matching-to-sample task prior to the onset of this experiment. At the beginning of each trial, the cursor and a fixation point (1.25 cm in diameter) would appear on the computer monitor. The fixation point was presented in the center of the computer monitor while the cursor was randomly positioned on the screen. Subjects were required to move the cursor into the exact center of the fixation point. Once this condition was met, then a randomly selected sample stimulus was presented for 500 ms either to the left or right of the fixation point. The sample stimulus was separated from the fixation point by 5 cm. After the sample stimulus was erased from the monitor, two comparison stimuli were randomly presented, one 5 cm above the fixation point and one 5 cm below the fixation point. The positive comparison stimulus was identical to the sample stimulus and the other stimulus was a nonmatching foil selected at random from the remaining three stimuli making up either stimulus set 1 or 2. Correct responses were defined as those trials on which the subjects moved their cursor to the positive comparison stimulus and were followed by auditory feedback and the delivery of food reinforcement. No reinforcement was provided and a raucous buzz was presented when the subject responded to the foil stimulus.

Each chimpanzee and monkey received 50 trials for each problem type (BOTH, GLOBAL, LOCAL) and stimulus library (libraries 1, 2, and 3). To obtain an equal number of data points for the latency data in each condition, errors were re-presented until 50 correct responses in each condition were obtained. The problem type variable was randomized across trials, whereas stimulus library was manipulated by blocks of trials. All subjects were tested on stimulus

¹The average number of trials to criterion for BOTH, GLOBAL, and LOCAL problems was 85, 108, and 201 for the chimpanzees and 174, 150, and 379 for the monkeys. For the generalization test, the average percent correct for BOTH, GLOBAL and LOCAL problems was 88, 77, and 77 for the chimpanzees and 71, 78, and 75 for the monkeys, respectively. We were not specifically interested in comparing performance on these data because the subjects had unlimited visual access to the stimuli and therefore, the duration of stimulus presentation time was not controlled between subjects.

libraries 1, 2, and 3 in that order. Position of the comparison stimuli (top vs bottom) and visual field of sample presentation (left or right) were randomized each trial. Accuracy and latency were the dependent measures. Accuracy was based on the subjects' percent correct on the first 50 trials presented for each problem. Latency was measured in hundredths of a second and was defined as the time elapsed between the offset of the stimulus presentation and the detection of a collision between the cursor and one of the comparison stimuli.

Results

For the test data, mixed-design analyses of variance (ANOVAs) were performed with accuracy and latency serving as the dependent measures. An average latency and accuracy value was determined for each subject by averaging its performance scores across the three stimulus libraries. This was done to reduce the number of variables in the model and therefore limit the probability of type I error. Pearson product-moment correlations revealed consistent individual performance between the three libraries (Lib) for both the accuracy ($r=0.81$, 0.57 , and 0.69 for Lib-1 and Lib-2; Lib-1 and Lib-3; and Lib-2 and Lib-3, respectively) and the latency data ($r=0.78$, 0.70 , and 0.75 for Lib-1 and Lib-2; Lib-1 and Lib-3; and Lib-2 and Lib-3, respectively). Problem type (BOTH, GLOBAL, LOCAL) was the repeated measure and species (chimpanzee, monkey) was the between-groups factor. Alpha was set at $P<0.05$ and all post hoc analyses were performed using Tukey's honestly significant difference (HSD; $P<0.05$).

Accuracy

With respect to the accuracy data, a significant two-way interaction was found between species and problem type [$F(2, 16)=3.94$, $P<0.04$]. For each species, the average percent correct as a function of problem type can be seen in Fig. 2. Post hoc analysis indicated that the chimpanzees performed significantly better than the monkeys on the BOTH and GLOBAL problems but not on the LOCAL problems. Additionally, the chimpanzees performed significantly better on the BOTH compared to the GLOBAL and LOCAL problems and significantly better on the GLOBAL compared to LOCAL problems. In contrast, the rhesus monkeys performed significantly better on the BOTH problems compared to the GLOBAL and LOCAL problems but did not differ in performance on the GLOBAL and LOCAL problems.

Latency

As with the accuracy results, a significant two-way interaction was found between species and problem type [$F(2, 16)=9.09$, $P<0.003$]. Depicted in Fig. 3 are the mean latencies as a function of problem type and species. Post hoc analysis indicated that latency for the BOTH, GLOBAL, and LOCAL problems differed significantly from each other for the chimpanzees with BOTH problems having the shortest latency and LOCAL problems having the longest latency. In contrast, for the rhesus monkeys, latencies were significantly shorter for the BOTH problems compared to the GLOBAL and LOCAL problems. No difference in latency was found for the GLOBAL and LOCAL problems for the rhesus monkeys.

Discussion

The results of this study indicate that chimpanzees and monkeys, under free viewing circumstances, selectively attend to different aspects of hierarchical compound stimuli. As has been reported in human subjects, chimpanzees exhibit a global-to-local precedence whereas monkeys do not. This conclusion is supported by both the accuracy and latency data as well as the trend analyses. It should be emphasized that both species could solve the discrimination problems but differed in their hierarchical processing of the perceptual attributes of these stimuli.

The species differences in processing of the hierarchical stimuli are consistent with recent findings in chimpanzees and baboons (Fujita and Matsuzawa 1988; Fagot and Deruelle 1997). Fagot and Deruelle (1997) found that humans and baboons differed in the processing of global/local stimuli not unlike those used in this study. The baboons performed better and faster on local trials compared to global trials. In contrast, humans exhibited the classic global-to-local precedence. Fujita and Matsuzawa (1988) have reported that the chimpanzee Ai was able to reconstruct visual-graphic symbols by pressing keys corresponding to the individual geometric elements that made up the symbol. Fujita and Matsuzawa (1988) reported that Ai tended to reconstruct the symbol by first reporting the outside elements followed by those that were located locally within the symbol. Whether the species differences are due to differences in the organizational properties of the sensory or perceptual system or in post-stimulus processing is not clear but this issue warrants further investigation. Our results also support the contention that monkeys, when performing discrimination tasks, selectively attend to the fine details of a compound stimulus and utilize these attributes in maintaining responding. Chimpanzees are less likely to adopt this type of information-processing strategy (but see Fagot and Tomonaga 1999); however, we would emphasize that any two stimuli that differ in their global characteristics by definition differ on the basis of features unless the stimuli are mirror-image stimuli. Thus, the letters “E” and “F” when constructed of the smaller letter “E” differ in that “E” has one more feature than “F” when not considering the smaller elements. It is perhaps the spatial separation of the elements that causes the monkeys to focus on the local elements whereas the chimpanzees tend to ignore the spatial separation and process the overall stimulus in some gestalt manner (see Wertheimer 1938).

A 500 ms presentation duration was used in this study and this may have differentially influenced the performance of each species on this discrimination task. For instance, rhesus monkeys and chimpanzees may differ in the amount of information they need to make a discriminative response. Rhesus monkeys may need more time to perceive and process a stimulus and therefore limiting the presentation duration may force the animals to rely on cues they normally would not use. The same stimulus presentation duration limitation may not influence performance by the chimpanzees, although it should be emphasized that chimpanzees do show the global-to-local precedence when stimuli are presented for 100 ms in duration (Hopkins 1997).

In conclusion, chimpanzees exhibited global-to-local precedence in the processing of compound stimuli whereas monkeys did not. Moreover, overall performance differed between species with chimpanzees performing better and responding faster than the rhesus monkeys. From these results, we would suggest that differences in learning among species may be fundamentally related to the manner in which they perceive and attend to attributes of compound stimuli, a factor often ignored or overlooked in comparative cognition research.

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Fig 1.
Stimulus libraries 1, 2, and 3

Fig 2. Average percent correct for chimpanzees and monkeys for BOTH, GLOBAL, and LOCAL problems presented within the sequential matching-to-sample task

Fig 3. Average latency for chimpanzees and monkeys for BOTH, GLOBAL, and LOCAL problems presented within the sequential matching-to-sample task