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Individual Differences in the Cognitive Abilities of Chimpanzees

Sarah T. Boysen

After more than three decades of study of the chimpanzee, led by the landmark fieldwork of Goodall and her associates (Goodall 1968, 1986; McGrew 1992) and by the equally significant work by pioneers intent on characterizing the behavioral and cognitive characteristics of this remarkable species in captivity (Yerkes and Yerkes 1929; Hayes and Hayes 1951; Kellogg and Kellogg 1933), the chimpanzee has emerged as an animal whose capabilities cannot be easily compartmentalized. The chimpanzee has demonstrated its diverse capacities and traditions in use of tools, patterns of grooming, use of food resources, and capacity for attention as well as diversity in personality and temperament (Boysen 1992b; de Waal 1982, this volume; McGrew 1992, this volume). Indeed, the phrase that best describes the range of chimpanzee features and the behavior represented across chimpanzee populations in the wild and in numerous captive environments is *remarkable variability*.

Remarkable variability, including behavioral plasticity and flexibility, characterizes the range of cognitive abilities and cognitive potential that we studied in an effort to better define the learning capabilities and information- processing capabilities of chimpanzees. The Primate Cognition Project was established in recognition of our common primate heritage to bring potential shared cognitive similarities and differences of chimpanzees and humans more sharply into focus.

The past decade in the field of comparative psychology has witnessed a resurgence of interest in cognition and the comparative study of cognitive processes (Boysen and Capaldi 1993; Honig and Fetterman 1992; Ristau 1991; Roitblat et al. 1984). Moreover, chimpanzees have been reported to show cognitive abilities that are not in evidence for other animals, with the possible exception of other apes. Those cognitive abilities include cross-modal matching of stimuli (Davenport and Rogers 1970), self-recognition (Gallup 1970, 1991; Lin et al. 1992; Parker 1991), tool use and construction (McGrew 1992), and social attribution processes not shown in monkeys (Povinelli et al. 1990; Premack 1986; Premack and Woodruff 1978). Additional highly sophisticated cognitive capabilities have been suggested for the chimpanzee (Premack 1976; Premack and Woodruff 1978) and, thus, chimpanzees may afford a unique model with which to study the comparative development of cognition.

The studies undertaken in our laboratory have explored a range of cognitive abilities and capacities in the chimpanzee, including recognition of individual humans and conspecifics, vigilance and attention; and number-related skills (Boysen 1992a; Boysen et al. 1987, 1989a, 1989b, 1990, 1993; Boysen and Capaldi 1993). While the chimpanzees exhibited success with most of the tasks that we presented to them, it became apparent early in training that our three original chimpanzees represented a unique constellation of temperament, personality, and learning styles (Boysen 1992b). While we needed to adhere to the same experimental procedures with each animal on a given task, we readily perceived differences in the relationship of each chimpanzee with its human teacher, in the individual chimpanzee's abilities, and in the animal's approach to learning. To ignore the animals' individuality would have been to deny the real contribution of individual differences to the experimental context. These individual differences were significant parameters for precisely the cognitive potential we hoped to study (Boysen 1992b; Oden and Thompson 1992).

Physiological Correlates of Social Recognition

The relationships between our animals were dramatically different and readily discernible, even with only three chimpanzees. The two males Kermit and Darrell are from the collection of the Yerkes Regional Primate Research Center, Emory University. They are six months apart in age and have been together since early infancy at the Yerkes Center. Upon arrival at Ohio State at ages 3 and 3 1/2, they had been housed together continuously. The young female Sheba was originally from the Columbus Zoo. At the time she joined the project at age 2 1/2, she was physically too small to be housed with the boisterous and much larger males. However, all three animals spent a significant portion of each day interacting with one other and their human teacher.

From the first introduction of Sheba to the males, Darrell was aggressive; he maintained an antagonistic attitude toward her for the next nine years. On the other hand, although physically smaller than and subordinate to Darrell at the time, Kermit was immediately protective of Sheba, literally shielding her body with his from Darrell's blows and bites. These reactions by both males were exhibited within the very first seconds of their introduction to Sheba. And, like the enduring reaction of Darrell toward Sheba, Kermit has remained protective and highly prosocial toward her for the same nine-year period. Similarly these chimpanzees clearly exhibited distinct likes and dislikes toward humans who visited or worked in the laboratory.

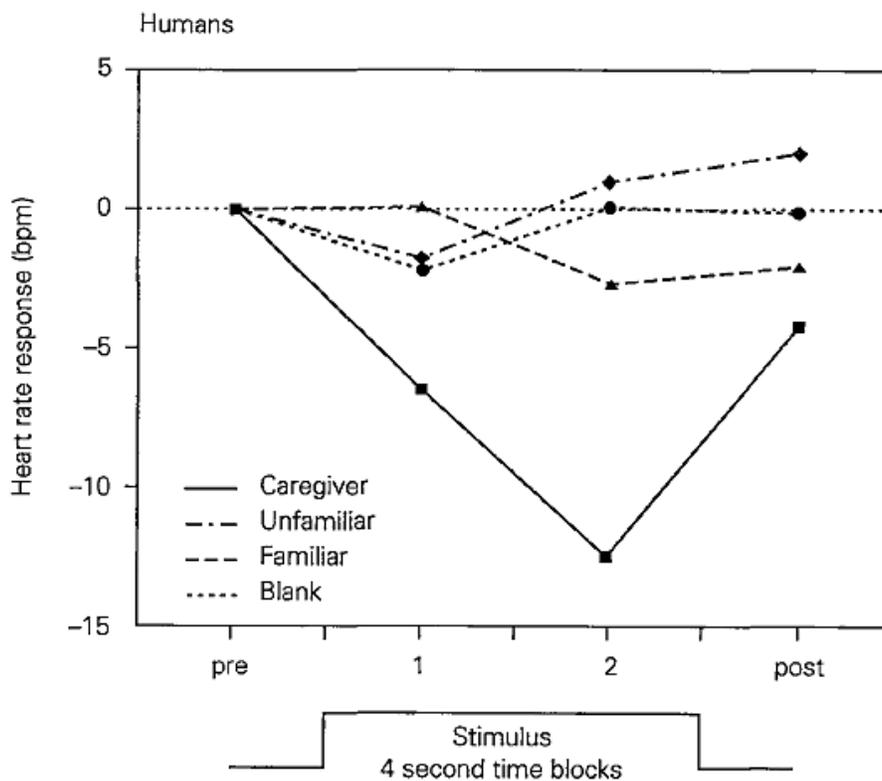
With these observations in mind, two studies were undertaken to explore underlying physiological reactivity to individual social relationships via cardiac measures. To explore a potential objective index of recognition of individuals relative to prior social experience, we recorded Sheba's heart rate as she viewed visual stimuli in the form of color slides in three social categories: her human caregivers, familiar individuals who she was likely to recognize but who were not directly involved in the project, and strangers; blank slides were used as a control (Berntson and Boysen 1986). Heart rate responses were recorded by disposable adhesive sensors attached to Sheba's chest and secured with a wide elastic bandage. Sheba required no pretraining for this procedure, and she readily cooperated in the preparation for recording her heart rate. We imposed no restraint (which we would not have done, despite our interest in the questions). The ease of testing and her apparent lack of concern for the recording apparatus and the attached sensors were likely supported by the strong bond between Sheba and her primary caregiver (Sarah Boysen), coupled with a gamelike approach to the task. For example, Sheba was provided with a full frontal view of herself in a large mirror, and she sought the opportunity to see herself.

We recorded Sheba's heart-rate responses to color slides of six human female faces in the three categories noted earlier and to blank control slides. Each slide was presented for eight seconds, with baseline heart rate recorded four seconds before, and twelve seconds after each slide was presented. Sheba simply sat and viewed the slides with an experimenter who was both unaware of the sequence of the slides and unable to see the projection screen. The results of the study revealed that heart rate responses were deceleratory to most slides (see figure 1) and that Sheba exhibited significant differences in her heart rate responses across the three categories. The most striking finding was Sheba's consistently larger deceleratory response to color slides of her caregivers.

The larger deceleratory heart rate response to the caregiver category appeared consistently over sessions, and to each of the individual color slides in this category, for an average of minus 9.4 beats per minute. The differential heart rate response was also apparent in measures of heart-period variability, reflected in a significantly longer deceleratory response to caregiver slides as compared with other slides. These changes in heart-rate response were not associated with any apparent pattern of overt behavioral change although, in one interesting instance, Sheba extended her hand toward the projected image of a caregiver.

These findings suggest that Sheba could recognize individuals from visual representations and that her heart rate might provide an objective measure of her social relationship with the individuals represented (Boysen and Berntson 1986). Most notably, these differences in heart rate response to the three social categories were exhibited in the absence of explicit training, task demands, or prior experience with slides of humans. The slower heart rate was likely part of an *orienting response* (Graham 1979), a response that is typically found associated with cardiac deceleration in numerous species including humans, apes, and monkeys (Graham 1979; Weisbard and Graham 1971; Boysen and Berntson 1984). Sheba's heart rate responses in this study appeared to be dependent upon the inherent significance of the slides, and those responses reflected her strong social bond with her caregivers. The results raised an obvious question. Would Sheba's heart rate patterns similarly reflect her dramatically different social relationships with the other chimpanzees in her group?

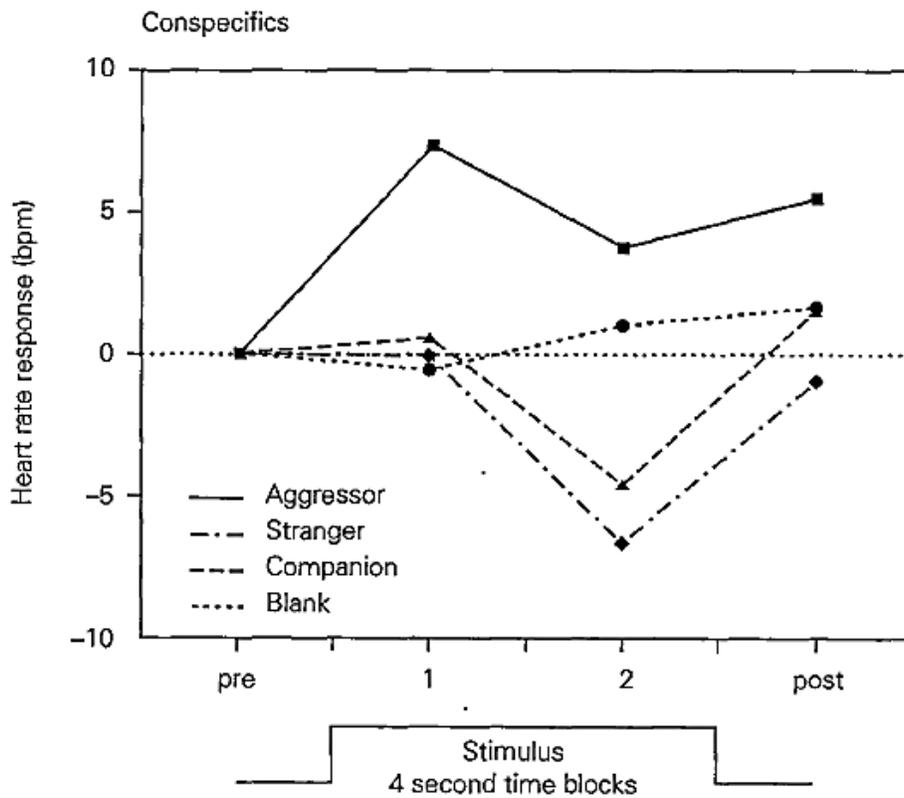
Figure 1. The heart rate response patterns are shown during slide presentations of human, categorized as caregivers, familiar individuals, strangers, and blank (white) control slides.



To answer the question, Sheba was given the opportunity to view color slides of chimpanzees in three social categories: an aggressor category represented by Darrell; Kermit, with whom Sheba shared a gregarious social relationship and who therefore represented a companion category; and an unfamiliar chimpanzee in the stranger category. Blank slides served as a control (Berntson and Boysen 1989a). The testing procedures were identical to those outlined for the human-recognition study. Similar to the findings from that experiment, Sheba exhibited consistent heart rate patterns to one category of slides. However, in contrast to the deceleratory responses exhibited when viewing the human caregiver slides, the significant heart rate response to a chimpanzee category was acceleratory (see figure 2). Moreover, this response was made only to slides of the aggressor Darrell, with whom Sheba had a long history of agonistic interactions, or conflicts.

The consistent acceleratory pattern likely represented a *defensive response*, a response that is exhibited under aversive or threatening circumstances (Graham 1979). We concluded that the defensive response to Darrell's slides reflected the aggressive and negative social relationship that Sheba and Darrell maintained and that the heart rate response was an objective, physiological reflection of their acrimonious history (Berntson and Boysen 1989a). Thus, both visual-recognition studies revealed that social history is a potent source of individual differences in chimpanzees. Social learning can powerfully shape the behavior, preferences, and dispositions of chimpanzees and humans alike. Even in the absence of genetic variation, differential social experiences would serve to carve individual features into the chimpanzee, given its exceptional behavioral plasticity.

Figure 2. The heart rate responses are shown during slide presentations of chimpanzees, including categories of Aggressor, Companion, Stranger, and blank control slides.



Cross-modal Recognition

Vocalizations in addition to physical features provide a rich source of information about individuals and play an important role in recognition. A number of species have been studied to determine if recognition of conspecifics through vocal input alone is possible (Cheney and Seyfarth 1980; Marler and Hobbett 1975; Snowdon and Cleveland 1980; Waser and Waser 1977). For example, several studies have demonstrated that human infants and juveniles respond selectively to vocalizations of their fathers (DeCasper and Prescott 1984) and that primate mothers respond differentially to vocalizations of their offspring (Kaplan et al. 1978; Newman 1985; Symmes and Biben 1985). Recognition of individual conspecifics may be particularly important among species such as chimpanzees who live in relatively large social communities. The ability to distinguish individuals in such a community would aid the

establishment and maintenance of critical relationships and alliances and would contribute to the overall stability of the group (de Waal 1982).

As demonstrated by Sheba, many primate species have shown the ability to recognize visual representations of other primates and objects (Bruce 1982; Davenport and Rogers 1970, 1971; Fujita and Matsuzawa 1986; Rosenfield and van Hoesen 1979; Sands and Wright 1980a, 1980b, 1982; Swartz and Rosenblum 1980). Moreover, Bauer and Phillip (1983) reported that chimpanzees learned to match an individual's facial portraits with that individual's corresponding pant-hoot vocalizations. However, no testing of transfer using novel stimuli was conducted and, thus, the generality of performance was unclear.

To further explore the capacity of the chimpanzee for cross-modal recognition, we used auditory and visual stimuli as follows: vocal greetings of humans were played during presentation of pictures of individual humans and chimpanzee food-bark vocalizations were played during presentation of pictures of individual chimpanzees (Nelson 1989). In addition, novel auditory and novel visual stimuli, different from the familiar stimuli employed in training, were used for testing.

Four chimpanzees participated in the study including Kermit who was 9 years old at the time of testing; Darrell, 9 1/2 years old; Sarah, 29 years old; and Sheba, 8 years old. Since their arrival at Ohio State, all the animals had participated in a variety of cognitive studies, and all had previous experience with mirrors, which they used for self-directed activities and for viewing one another from adjacent cages. Darrell and Kermit were housed in the same cage regularly, as were Sarah and Sheba, but on occasion each animal had been with the other chimpanzees for limited play sessions. In addition, they had all spent repeated, brief periods of time (one to four hours) housed together in the same cage.

Front and lateral views of the faces and heads of three familiar persons were used as visual stimuli for training and testing. Those six visual images were used in two forms; as separate color photographs, which could be presented one-by-one by an experimenter, and as slides. The slide images were presented three at one time with one blank slide as a control in a two-by-two matrix of four quadrants on a color television monitor. All possible combinations of the six images were presented in counterbalanced order and position on the color monitor. The response apparatus consisted of a touch-sensitive frame (Carroll Touch-Screen) that was placed over the color monitor and linked to a microcomputer that recorded and stored the responses.

Initial training involved two sets of simple matching tasks. The animals were required to choose the slide image presented on the color monitor that matched a color photograph presented by the experimenter. Subsequently, cross-modal matching of auditory and visual stimuli was required. A 15-second recording of a vocal greeting by one of the familiar persons was presented; the animal's task was to select the photograph that represented the person giving the recorded greeting. Throughout the phases of the study, photographs of three humans were presented on the monitor during each trial, with the fourth quadrant of the screen blank, and order and position of the visual stimuli counterbalanced over trials.

The second phase of this experiment employed the slide images instead of the color photographs that had been used previously as visual stimuli. Prerecorded vocalizations by each of the three individuals were now presented on a given trial. These auditory stimuli were presented immediately prior to presentation of the slide matrix, with vocal segments consisting of a brief greeting that had been matched for sound level and duration. The chimpanzees received 20 trials in each daily session until they were performing consistently at levels greater than chance.

The third phase of this experiment evaluated the chimpanzees' capabilities for transferring cross-modal matching skills to novel stimuli. The slide matrices were modified to include three novel stimuli, which were visual images of different, but familiar, persons. These novel stimuli were randomly placed in five of the 20 trials. The testing procedure using novel stimuli was the same as the training phases, with the exception that the experimenters gave no guidance or feedback.

Results

In reviewing the results of these experimental phases, the results of the match-to-sample training, during which the animals were required to match the slide image to a photograph, revealed considerable variability in the day-to-day performance of each chimpanzee. Although each animal exhibited a clear trend toward continued improvement across sessions, each varied considerably in their rate of acquisition. For example, Kermit and Sarah required only 20 daily sessions to reach a criterion of 85% correct responses over two successive sessions, while Darrell did not reach the same criterion until day 52, and Sheba needed 72 days.

These differences in performances were intriguing, particularly given Kermit's history of measurable attentional difficulties (Boysen 1992b). "When Kermit was tested on a vigilance task developed for very young children with Attention Deficit Disorder, his performance was compromised if the stimulus items appeared in degraded form or in very rapid succession. These changes in the task produce performance deficits in children with demonstrated learning disabilities (O'Dougherty et al. 1988). Thus, Kermit's attention deficits impacted on his ability to perform tasks that required sustained attention. However, in the case of the match-to-sample training with photographs, Kermit's performance proved superior to that of Darrell and Sheba, who typically outperformed the other animals on most tasks.

In the match-to-sample cross-modal training phase, the sample photographs were replaced by audio stimuli, and the animals were required to match vocalizations to an individual depicted on the color television monitor. Again, the animals varied considerably in the number of trials required to reach criterion. For example, both Kermit and Sarah required 60 daily sessions, while Darrell reached criterion after only 28 sessions, and Sheba, who had performed the most poorly on the initial match-to-sample task, met criterion in only six sessions.

In the third phase, the match-to-sample transfer test entailed the addition of random trials containing novel visual stimuli and corresponding novel auditory stimuli embedded within the videotaped matrices that had been used during training. Of the four animals, only Darrell exhibited a statistically significant performance with the novel stimuli within the first five trials, and he was correct on each novel trial. For all animals, performance in the first two sessions with the novel stimuli approximated the performance with the familiar stimuli (55% for novel tests, 59% for familiar stimuli). (See table 1). Analysis of all test trials across sessions revealed that three animals (Sheba, Kermit, and Darrell) were performing well above chance levels, while one animal (Sarah) was performing only marginally above chance. Performance on training stimuli throughout the ten sessions was maintained at significant levels by all animals, although Kermit's performance declined over the last several sessions.

The second experiment of the study consisted of a transfer test in which the novel stimuli depicted conspecifics. In this study, images of the four chimpanzee subjects were presented on a color monitor in a matrix of four quadrants, and recordings of food-bark vocalizations of Darrell and Sheba were played. The animals were initially tested using two different vocal segments from Darrell and two different vocal segments from Sheba for 10 sessions of 20 trials per session, a total of 200 trials per animal. The animals then completed an additional block of five sessions of 20 trials per session for a total of 100 trials, during which four novel vocalizations (two different vocalizations from Kermit and two different vocalizations from

Sarah) were presented as test stimuli. In this transfer test with conspecifics, Sheba and Kermit both performed significantly above chance in the first session, and Darrell's performance reached significance after two sessions. Evaluation of overall performance across the first 10 sessions revealed that each animal was performing above chance (see table 2). Darrell, Sheba and Sarah demonstrated significant improvement in performance from the first five-session block to the second five-session block, while Kermit maintained his initial accuracy throughout all 10 sessions. Considerable day-to-day variability was apparent in the performance of each animal.

Table 1. Transfer test with novel human photographs and vocalizations of humans.

Subjects	Sessions 1-5 (%)	Sessions 6-10 (%)	Overall performance (%)
Darrell	76*	64*	70*
Kermit	52**	64*	58*
Sarah	48	48	48
Sheba	64*	72*	68*

Notes: * $p < .001$ ** $p < .05$

An analyses of errors revealed that Darrell was the only subject to demonstrate a significant bias relating to position, making significantly more errors in the lower-left quadrant and significantly fewer errors on the upper-right quadrant. A bias relating to stimulus was also observed for Kermit and Sheba: Kermit made significantly more errors by selecting the image of Sarah and significantly fewer errors by selecting the image of Darrell. Sheba, in contrast, made a significantly more errors selecting the image of Darrell.

Table 2. Novel transfer test for cross-modal recognition of chimpanzees.

Subjects	Sessions 1-5 (%)	Sessions 6-10 (%)	Overall performance (%)
Darrell	49*	59*	54*
Kermit	41**	46*	44*
Sarah	35**	45**	40**
Sheba	48*	61*	55*

Notes: * $p < .001$ ** $p < .05$

Transfer to the remaining novel stimuli in the last five-session block proved to be relatively rapid for each animal (see table 3). In the first session, Darrell, Kermit, and Sarah each responded with significant accuracy. Sheba's performance reached statistical significance within the first two sessions. Performance across all five sessions of this transfer test was maintained at greater than chance levels by each subject.

In light of these experiments, evaluation of the ability to recognize both humans and other chimpanzees cross-modally through auditory and visual representations revealed that these chimpanzees were capable of matching visual images of humans and conspecifics to the appropriate vocalizations and that they could do so with considerable accuracy. Moreover, after initial training, three of the four chimpanzees demonstrated efficient transfer to novel auditory and visual stimuli that represented humans. Generalization to cross-modal matching of visual images and vocalizations of conspecifics was similarly rapid. In a final transfer phase, three of the four chimpanzees responded accurately to novel auditory and visual stimuli representing conspecifics during the first session, and the fourth animal reached significance after two sessions.

While no consistent pattern of errors was apparent, errors were not randomly distributed. One source of errors was likely related to attentional variables, particularly for those animals with a prior history of

attentional difficulties (Kermit and, in some cases, Sarah). Each animal demonstrated lengthy runs of consecutive correct responses throughout testing, with errors also tending to occur in consecutive trials. In addition, considerable session-to-session variability was observed, with incorrect choices often associated with signs of distraction or lack of attention to the task, such as moving away from the testing area or failure to orient to the test display.

Table 3. Novel generalization test for conspecific visual/auditory recognition.

Subjects	Correct Response (%)
Darrell	54
Kermit	59
Sarah	53
Sheba	66

Note: Total trials = 100

Considerable differences existed in the prior social interactions between the animals, although this did not appear to be a primary determinant of response biases. Darrell and Kermit were generally housed together, as were Sarah and Sheba. Nevertheless, response biases were not clearly related to these housing conditions or to prior social history. Thus, while Kermit made significantly fewer errors on stimuli depicting Darrell, both Sarah and Sheba demonstrated a similar pattern of performance. Moreover, during the final test phase, Sheba made a significant number of errors by choosing her own image. Each apparent stimulus bias in the final transfer concerned stimuli that had been reinforced, indicating that interference from a previous phase may have contributed to these incorrect choices. However, because the transfer tests in the cross-modal study employed novel auditory and visual stimuli, the chimpanzees could not have responded on the basis of previously formed associations.

Thus, the present findings appear to reflect a robust capacity for visual-auditory, cross-modal recognition in the chimpanzee. These data suggest that chimpanzees possess the capacity to form sufficiently rich auditory and visual representations of individual humans and other chimpanzees, as well as of themselves, to permit such cross-modal recognition. The fact that each subject was capable of recognizing individuals depicted in color slides and sound recordings, both of which are inherently impoverished representations, indicates that the recognition of individuals may be a relatively fundamental capacity of chimpanzees. Moreover, each animal's capability of correctly matching novel visual stimuli and novel auditory stimuli in transfer tests suggests that each animal may have previously established cross-modal identifications.

Concluding remarks

A variety of studies using our chimpanzees have revealed various individual strengths and weaknesses with respect to specific cognitive capabilities in some testing contexts among these subjects. Had Kermit been our only subject, our conclusions regarding the cognitive dynamic of the chimpanzee may have been quite different. In view of such considerations, an appreciation of the capacity for attention, developmental and experiential histories, and the temperament style of individual animals appears to be important in the interpretation of behavioral studies and, consequently, in the comparative evaluation of cognitive processes of apes.

For example, over the past year, following significant renovation of the chimpanzee housing area that has permitted our chimpanzees to interact as a group for the first time, Kermit's performance on some tasks has been dramatically enhanced. As noted earlier, Kermit and Darrell had been housed together

continuously since infancy. A group of three other chimpanzees formed over the years as additional animals arrived. Thus, at 28 years of age following a lifetime of species isolation at another laboratory where other chimpanzees could be seen but not interacted with, Sarah was introduced to 6-year-old Sheba. Two years later, 3-year-old Bobby joined this pair. All five chimpanzees were introduced to one another following the laboratory renovation, and they now spend every day together.

Darrell had been dominant to Kermit for the past decade prior to the renovations. We predicted a change in their rank when the females began interacting directly with the two males, when Kermit's massive increase in size after adolescence size became apparent. Prior to the renovation, the two groups of chimpanzees had very limited visual access and no physical access to each other. Following renovation, when the two groups were introduced, the females' became increasingly solicitous, particularly to Kermit, and he did emerge as the dominant male.

Other changes in Kermit ensued after the renovation. Most interesting was Kermit's remarkable new ability to acquire number concepts, despite five to six years of continuous training that had yielded essentially no stable and definitive understanding of number and quantity associations. Variables other than changes caused by the renovation also likely impacted on Kermit's recent acquisition of number relationships. Among these variables was the addition of a computer-interfaced, touch-frame testing system that very likely provided Kermit a structure for greater attention to the task. However, his concomitant rapid change in social rank, power over the group, and enhanced control over his environment have also very likely contributed in immeasurable ways to his new abilities to acquire number concepts. Given the flexible social structure of chimpanzees in the wild and in captivity, each individual makes a potentially significant contribution toward cooperative social living. Such contributions are readily revealed within even the small social group studied in our laboratory.

In many respects, the range of conceptual tasks offered in our laboratory and the chimpanzees' resulting opportunities to demonstrate differing abilities have provided a rich picture of the range of capabilities in individual chimpanzees as well as new insights into the potential cognitive capacities of chimpanzees in general. Thus, focusing on only a singular chimpanzee, a singular approach, or a singular task, while perhaps providing evidence for a particular skill or related skills, may limit the questions that can be explored in attempting to characterize the cognitive domain of the chimpanzee.

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