The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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26 The Evolution and Ontogeny of Ordinal Numerical Ability

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It is generally assumed that the development of human mathematical reasoning requires years of schooling. That being the case, mathematical reasoning would seem beyond the reach of the rest of the animal kingdom. This commonsensical conclusion poses an issue that is the focus of this chapter. What, if any, evolutionary precursors of human mathematical reasoning can be observed in animals?

To answer that question, we must first recognize that human mathematical ability is composed of many heterogeneous skills. Humans use symbols to represent numerosities and to represent operations such as addition and division; they are capable of manipulating numerical symbols in complicated ways (e.g., algebra and the calculus). It is even more important to recognize that the most basic numerical skills do not require *any* numerical symbols. It is, for example, possible to discriminate the relative numerosity of two sets of objects without the help of numerals (e.g., that a collection of 4 peanuts is numerically larger than a collection of 2 apples).

During the past 30 years, investigators of animal behavior have shown that many species possess some numerical ability (for reviews see Davis and Perusse 1988; Roberts 1997). Those observations have led some psychologists to hypothesize that human mathematical ability evolved from numerical abilities that can be observed in animals (Dehaene 1997; Gallistel and Gelman 1992, 2000). Our research program on the ordinal numerical abilities of rhesus monkeys has provided considerable evidence in support of that hypothesis (Brannon and Terrace 1998, 1999, 2000). As background, we first describe other experiments that have addressed this topic and show how our approach differs. We then discuss aspects of a monkey's numerical behavior that appear to be analogs of mathematical thinking in adult and developing humans. Finally, we define some promising future directions for research.

If monkeys use number to organize events in their natural environment, we should expect them to represent number on at least an ordinal scale. They should not only be able to differentiate n versus m objects, but they should also appreciate that a collection of $n + m$ objects is numerically greater than n objects. Thomas and colleagues (1980) tested this idea in an experiment in which squirrel monkeys were trained to respond to the lesser of two numerosities. The values of the numerosities were increased progressively as the monkeys learned each pair. Although Thomas et al. provided impressive evidence that squirrel monkeys could discriminate sets containing as many as 10 and 11 elements, it was unclear whether their subjects used an ordinal rule to solve each pair, or whether they had learned a series of pairwise discriminations, for example, that 4 is rewarded when it is paired with 5, but not when it is paired with 3. The latter interpretation cannot be ruled out because the pairs of numerosities were trained successively, one pair at a time.

Washburn and Rumbaugh (1991) used a different paradigm to investigate the numerical abilities of rhesus monkeys. In each trial they presented a pair of Arabic numerals whose values ranged from 1 to 9. The monkeys learned to choose the larger numeral and even responded correctly when novel combinations of Arabic numerals were tested. Although the monkeys learned to choose the larger numeral when it was presented in a novel pair, it does not follow that they learned a symbolic numerical rule. The monkeys' choices could have been based on the hedonic value associated with each of the numerals (yummie versus very yummie; also see Olthof et al. 1997). To show that the monkeys associated a discrete number of pellets with each Ar-

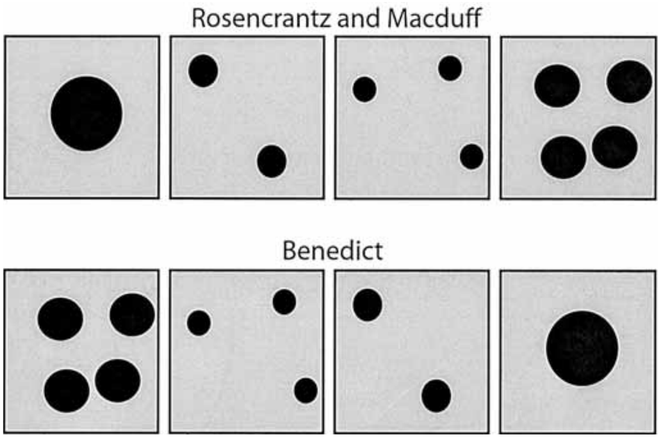

Figure 26.1
Example of one stimulus set. Rosencrantz and Macduff responded in ascending order (1-2-3-4) and Benedict in descending order (4-3-2-1). Stimuli were presented in a random configuration on a touch-sensitive computer monitor. Many different stimulus sets were used, only one of which is shown here.

abic numeral, it would be necessary to test them with a paradigm that provided the same amount of food for each correct choice.

Other investigators have used a forced-choice discrimination procedure to study ordinal numerical knowledge (Meck and Church 1983; Roberts and Mitchell 1994; Emmerton et al. 1997). In these studies rats and pigeons were trained to make one response to a small number of stimuli (sounds and/or light flashes) and another response to a larger number. When subsequently tested with intermediate numerical values, the probability of making the large number response depended on the ratio of the intermediate value to the trained anchor (small and large) values. The confusions of magnitude produced by this paradigm provide an indirect measure of knowledge of numerical order.

However, for a more direct test of an animal's knowledge of numerical order, it is necessary to train subjects to order values in one numerical range and then test their ability to order values outside that range. Without such tests, one cannot distinguish between knowledge of an ordinal rule and memory of a set of pairwise categorical discriminations as a basis for accurate responding to novel pairs of numerosities. To distinguish between those possibilities, we performed an experiment (Brannon and Terrace 1998) in which we trained three monkeys to order the numerosities 1, 2, 3, and 4 in an ascending or descending order (see figure 26.1). Exemplars of the numerosities 1, 2, 3, and 4 were selected from a large library of stimuli in which surface area was varied systematically to ensure that it could not serve as a cue for number. The monkeys were first trained on 35 different sets of the numerosities 1–4. The same numerical stimuli were used in each trial, albeit in randomly selected physical configurations. The monkeys' performance improved dramatically over the 35 training stimulus sets. On average, the monkeys responded in the correct order on 45 percent of the trials on the final 10 training sets (chance level of accuracy ~4 percent).

To rule out the possibility that the monkeys had memorized each of the 35 stimulus sets and the order in which to respond to each set, we

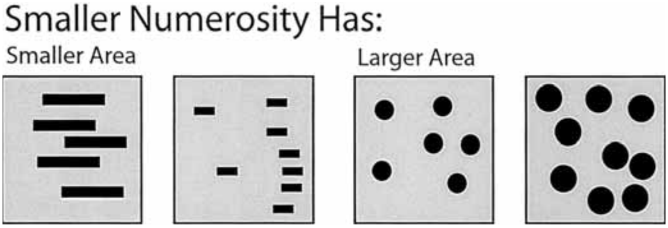

Figure 26.2
Example stimulus sets used in numerical comparison task with monkeys and humans. On half of the trials, the smaller numerosity had a larger cumulative surface area.

tested their ability to order 150 novel sets of the numerosities 1–4. Each novel set was presented only once. The subjects continued to respond at approximately the same level of accuracy (40 percent) even though they had no opportunity to memorize any of the novel stimulus sets. The absence of a decrease in performance with the novel stimulus sets provided clear evidence that the monkeys used the numerosity of each stimulus (as opposed to some non-numerical memory strategy) to determine the order in which to respond to the stimuli from each set.

Less clear is *how* the monkeys represented the order in which to respond to the numerosities 1–4. One possibility is that the monkeys assigned each numerosity to one of four distinct nominal categories. In this scenario, the monkeys would have learned an arbitrary ordering of the four categories, just as if we had taught them to respond to different exemplars of, say, birds, flowers, trees, and rocks. In this view, it should be just as easy for monkeys to respond in an arbitrary numerical order such as 3-1-4-2, compared with 1-2-3-4 or 4-3-2-1. Contrary to that hypothesis, one of our subjects (Macduff) showed no signs of improvement on a 3-1-4-2 sequence after training on 13 stimulus sets (see figure 26.2 for example stimulus sets) (Brannon and Terrace 2000). However, Macduff's performance rapidly improved once he was required to respond in an ascending numerical order. The ease of learning monotonic rules, compared with nonmonotonic rules, strongly suggests that monkeys perceive the ordinal relations between the numerosities on which they were trained.

In our next experiment we used the same subjects to evaluate more directly a monkey's ability to perceive ordinal relations between novel numerosities. The subjects were tested on their ability to order pairs of novel numerosities according to the ascending or descending rule they had learned previously with respect to the numerosities 1–4. The test consisted of exemplars of all possible pairs of the numerosities 1–9 (see figure 26.2). The monkeys trained to respond 1-2-3-4 were expected to respond in an ascending order to the new pairs (e.g., 4 then 7 or 5 then 9) and the monkey trained to respond 4-3-2-1 was expected to respond in the reverse order. Reinforcement for correct responding was available only on trials in which the pairs were composed of familiar numerosities (1-2, 1-3, 1-4, 2-3, 2-4, 3-4). In trials on which a novel numerosity was presented, no positive or negative reinforcement was provided, and the monkeys were permitted to respond in either an ascending or a descending order. This prevented subjects from learning the ordinal relationships between novel numerosities.

Rosencrantz and Macduff, the monkeys who had been trained to respond to the numerosities 1–4 in an ascending numerical order, responded correctly on approximately 75 percent of the trials composed of two novel numerosities. Both

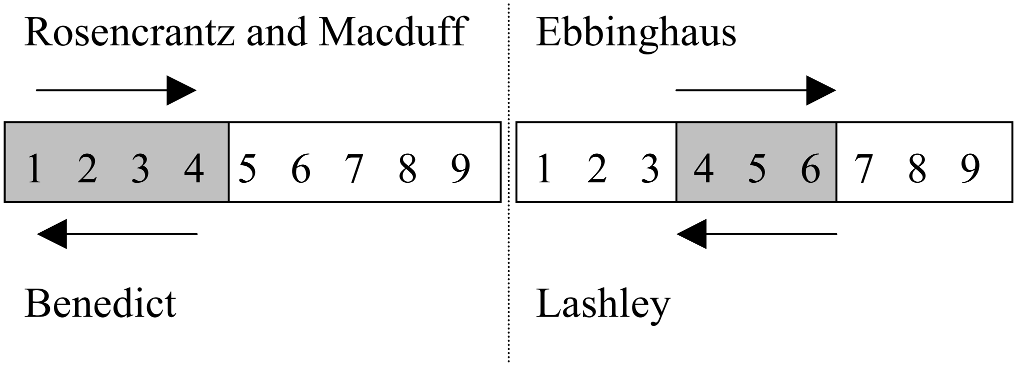

Figure 26.3
Schematic diagram of the experimental design. The shaded values were used in training. One monkey was trained to respond 4 then 5 then 6 and the other monkey was trained to respond in the reverse order. Both monkeys were then tested on all possible pairs of the numerosities 1–9.

subjects were just as accurate on pairs for which the larger numerosity covered a smaller area as on pairs for which the larger numerosity covered a larger area. Since neither subject had any previous training with the numerosities 5–9, their ability to respond to those numerosities in an ascending order provides clear evidence that a monkey can extrapolate an ascending rule to novel numerosities.

Curiously, Benedict, the single monkey who learned to respond in a descending order (4-3-2-1), did not exceed a chance level of accuracy on pairs of novel numerosities (Brannon and Terrace 2000). Since Benedict was the only subject who learned a descending sequence, it was unclear whether his inability to order novel numerosities was idiosyncratic or whether it was a consequence of learning a descending rule. Even if individual differences could be ruled out, it remained unclear why knowledge of an ascending rule should enable a monkey to extrapolate that rule to novel numerosities and why knowledge of a descending rule should not.

To address that question, we recently trained two rhesus monkeys to respond to the numerosities 4, 5, and 6, one in an ascending order (Ebbinghaus); the other in a descending order (Lashley), and then tested them on all possible pairs of the numerosities 1–9 (Brannon et al. in preparation; Kovary et al. 2000). This design (which is shown schematically in figure 26.3) creates novel numerical values that are both smaller and larger than the training values.

Both monkeys learned to respond to the stimulus sets composed of the numerosities 4, 5, and 6 in the required order. In each instance, however, accuracy with pairs of novel numerosities varied systematically with the relationship between the values of the novel numerosities and the initial value of the sets used to train the ascending and descending rules (see figure 26.4). For example, Ebbinghaus, who was trained on the ascending rule 4-5-6, responded at a high level of accuracy with the pairs 7-8, 7-9 and 8-9, but performed at chance levels of accuracy with the pairs 1-2, 1-3 and 2-3. Conversely, Lashley, who was trained on the descending rule 6-5-4, responded at a greater than chance level of accuracy with the pairs 3-1, 3-2, and 2-1, but at chance levels of accuracy with the pairs 9-7, 9-8, and 8-7. This pattern of results suggests that when ordering two novel numerosities, the sub-

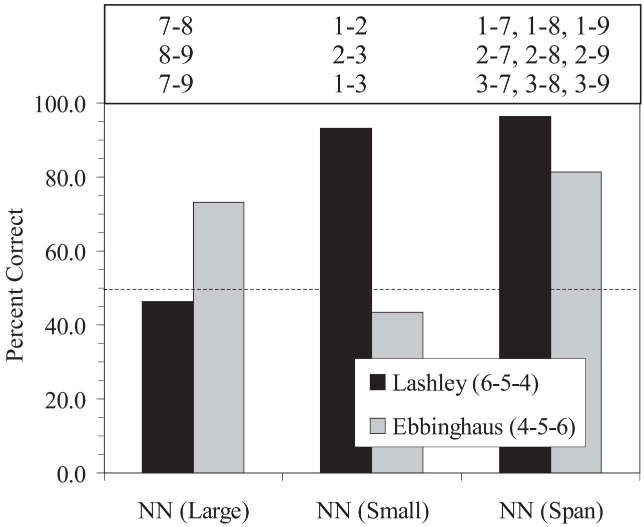

Figure 26.4
Performance on ordinal comparisons of two novel numerosities for monkeys trained on a 4-5-6 or 6-5-4 rule. Performance is shown separately for pairs that were composed of two values smaller than the training values (NN small), two values larger than the training values (NN large), and pairs that included one small and one large value (NN span). Note that performance on pairs composed of two familiar values or one familiar and one novel value is not shown here, but was high for both monkeys (range 75–85 percent).

jects compared each novel value with a representation of the initial value of the training set (e.g., 4 for Ebbinghaus and 6 for Lashley). That rule can also account for Benedict's failure to order the novel numerosities 5–9 after being trained on sequences of 4-3-2-1.

In an effort to further assess the possible link between nonhuman primate and human numerical representations, we investigated whether the well-established numerical distance effects found with adult humans are also found when nonhuman primates make numerical comparisons. Distance and size effects are found in a wide variety of circumstances when adult humans make numerical comparisons (e.g., Moyer and Landaeur 1967; Hinrichs et al. 1981; Tzeng and Wang 1983; Dehaene et al. 1990). Reaction time decreases with increases in the numerical distance between a pair of Arabic numerals and increases as the absolute size of their value increases. Similar distance and size effects have been reported when adults compare the numerosity of collections of dots (Buckley and Gilman 1974). If monkeys and humans rely on a shared system for judging relative numerosity, we should expect to find similar effects in both species with respect to the accuracy and reaction times of numerical comparison judgments.

We tested this hypothesis in an experiment on college students using the same pairwise numerical comparison task and the same stimuli that we used with monkeys. The subjects were given verbal instructions to respond first to the stimulus with the fewer number of elements and to respond as quickly as possible while not making too many errors. As can be seen in figure 26.5, numerical distance and size had similar systematic effects on the reaction times and accuracy

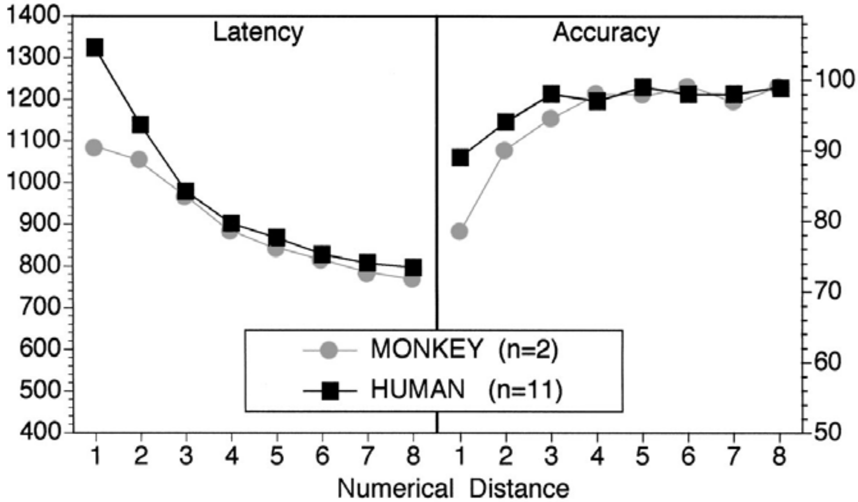

Figure 26.5
Latency to the first response (left) and accuracy (right) in a pairwise numerical comparison task as a function of numerical distance. Monkeys (Rosencrantz and Macduff: circles) and humans (squares) were required to respond first to the stimulus with the fewer number of elements.

levels of both college students and monkeys (E. M. Brannon and H. S. Terrace, unpublished). These data provide compelling evidence that animals and humans use the same numerical comparison process (see Whalen, Gallistel, and Gelman 1999).

What do the numerical distance and size effects tell us about the format of numerical representations? Just as Weber's law applies to perceptual discriminations of continuous dimensions such as line length and weight (Welford 1960), it also applies to numerical discriminations (Moyer and Landaeur 1967). This suggests that animals and humans rely on analog representations of number. The idea is that sets of discrete stimuli are converted into continuous-magnitude representations before the comparison process takes place (Gallistel and Gelman 2000).

If there is an analogical numerical processing system in animals and adult humans that is independent of language, at what point in development does it arise? E. M. Brannon recently investigated the existence of ordinal numerical knowledge in children 2 years of age who had not yet mastered the verbal counting system (Brannon and Van de Walle 2001). The children were tested with a simple game in which two trays were presented that contained one and two boxes, respectively. The tray with two boxes was designated as the winner and a sticker was hidden beneath each box. The children were asked to choose the winner tray to receive the stickers. After 5–10 trials of the 1 versus 2 comparison, the children were then tested with new numerosities. The results indicated that they were able to choose the larger numerosity on more trials than would be expected by chance, even when the size of the boxes was varied so that number was not confounded with surface area. This suggests that even before children learn how to count verbally, they have an appreciation of the ordinal relations between numerosities (see also Bullock and Gelman

1977). Research in many different laboratories is currently investigating how early in development this ordinal numerical knowledge is in place (see Brannon in press, Feigenson et al. in press).

In summary, the data reviewed reveal the similarities in the ways adult humans, animals, and children compare numerosities. Whether the similarities between humans and animals result from convergent evolution or reflect homologous processes is not yet known. Similarly, whether the numerical abilities demonstrated in infants and young precounting children are the foundation out of which the verbal counting system develops is not yet known (Carey 1998). We do not yet understand the processes that animals, infants, or adults use to enumerate nor do we understand the steps of the numerical comparison process. For example, do monkeys employ a serial countinglike process? Do infants serially scan the elements in a display when making discriminations of 2 versus 3 or 8 versus 16 dots (e.g., Strauss and Curtis 1981; Xu and Spelke 2000) or do they instead use a parallel enumeration process (e.g., Dehaene and Changeux 1993)?

Another important unanswered question is whether the same neural circuitry supports ordinal numerical comparisons in animals and humans. Neuropsychological and brain-imaging studies implicate the parietal lobe in nonverbal approximate number knowledge in adult humans (see Dehaene 2000 for a review). However, almost nothing is known about the neural underpinnings of numerical abilities in animals and human infants. Identification of the brain circuits involved in numerical behavior in animals and human infants promises to shed light on whether animals, human adults, and human infants share a numerical processing system.

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