Animal Arithmetic

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Non-humans Represent 'Numbers'

Early reports of animal numerical abilities argued that number is an unnatural dimension for the animal mind. These early studies by Davis and Perusse claimed that an animal can only conceive of numerical values after extensive training in a laboratory. For example, Davis and Perusse once argued that if a rat or pigeon is given a judgment task testing stimuli that vary in size and number, the animal will base its judgment on size rather than on number. In this view, a proclivity to use numerical concepts is a uniquely human phenomenon. However, since these early studies, many studies have established that animals other than humans represent numerical values, and in many cases, they do so spontaneously.

Animals as different as bees, fish, salamanders, birds, raccoons, rats, lions, elephants, and primates have been shown to make quantity discriminations. We can infer from this vast and diverse set of studies that all animals reason about quantities to some extent. Moreover, several studies such as those by Marc Hauser and Karen McComb suggest that animals attend to the quantitative attributes of their world naturally, spontaneously, and automatically. In the wild, groups of lions and chimpanzees naturally avoid unfamiliar groups of their conspecifics when they are outnumbered. Honeybees have been shown to use the number of landmarks (e.g., trees) that they pass along their foraging route to locate a feeding site. Salamanders preferentially choose feeding sites with large amounts of food (fruit flies) over small amounts of food. And female mosquitofish show a natural preference for joining a school with a larger number of fish in order to avoid sexually harassing males. Thus, animals of all types spontaneously use quantitative information to make adaptive decisions in their natural environments.

Laboratory studies by Cantlon and Brannon also indicate that animals have a spontaneous capacity for representing numerical values. In contrast to many prior naturalistic reports, these laboratory studies ensured that animals truly represent 'number' as opposed to some other quantitative dimension such as size. This level of control is important in order to determine whether animals are using pure numerical representations to make quantitative judgments instead of the total size or extent of the set (e.g., the cumulative surface area of the set). Under some circumstances, the number of items in a set is in quantitative conflict with the total size or extent of the set. For example, a group of six lions is numerically greater than a group of three elephants but, the group of three elephants takes up more space and has a greater cumulative surface area than the group of lions. This fact raises the question of whether animals use number and/or spatial extent to make quantitative decisions.

In a recent laboratory study, Cantlon and Brannon tested monkeys with and without prior numerical training on a numerical matching task to determine whether explicit training is necessary for animals to conceive of numerical values. Number-experienced and number-naïve monkeys were tested on a matching task in which they were allowed to freely choose the basis for matching from two dimensions: number, color, shape, or cumulative surface area. During this task, number was confounded with one of the other three alternative dimensions. For example, as shown in **Figure 1(a)**, in the shape and number condition, if a sample array contained two circles, the monkey would then have to choose between two circles (shape and number match) and four lightening bolts (shape and number mismatch) to find a match. The correct match could have been made on the basis of either number or shape, or both. Because number was always confounded with an alternative dimension during training, there was no explicit training for the monkeys to use number as the basis for matching. In fact, the monkeys could have completely ignored the numerical values of the stimuli and solved the task using the alternative dimension.

After each monkey could successfully solve the matching task, probe trials were introduced in which number was pitted against the alternative dimension (color, shape, or surface area) as shown in **Figure 1(b)**. The monkeys now had to choose which dimension they preferred as the basis for matching: number or color, shape, or surface area. During these probe trials, the monkeys were rewarded no matter which option they selected as the match so that they could freely indicate the dimension that guided their decisions. Remarkably, both number-experienced and number-naïve monkeys chose to match the stimuli on the basis of numerical value across a substantial proportion of the probe trials. These findings demonstrate that pure numerical value is a salient feature of the environment for monkeys, regardless of their prior training experience. Claims that 'number' is an unnatural dimension for the non-human animal mind are therefore false.

Taken together, studies of many different species using many different experimental protocols firmly indicate

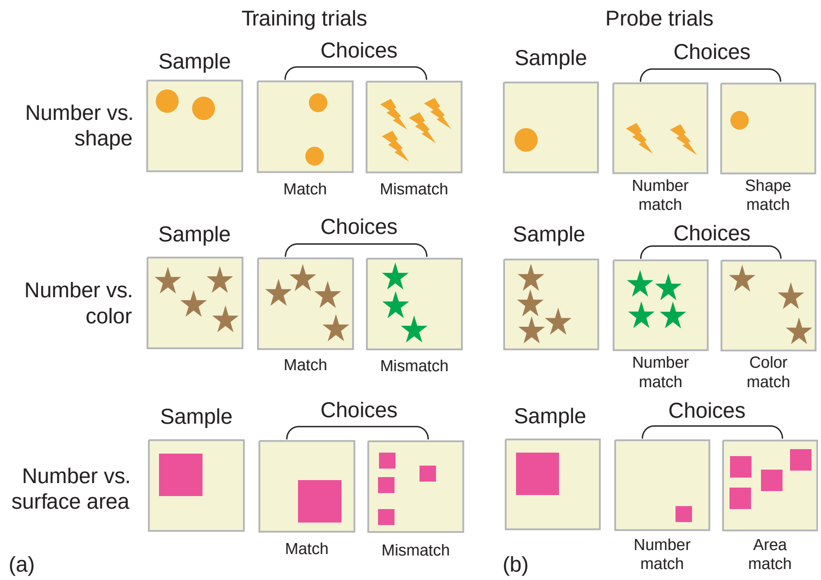

Figure 1 Monkeys were trained to match stimuli (a) in which numerical value was confounded with a second dimension of shape, color, or surface area Cantlon and Brannon (2007). Then, they were tested on the same task with probe stimuli (b) in which numerical value was in conflict with each of these three dimensions. Even though this training did not require monkeys to use number (because they could always use the alternative dimension of shape, color, or surface area), the data from probe trials indicated that they did use number to solve the matching task. Redrawn with permission from Cantlon JF and Brannon EM (2007). How much does number matter to a monkey? *Journal of Experimental Psychology: Animal Behavior Processes* 33(1): 32–41.

that non-human animals represent numerical values. Yet, such evidence does not imply that non-human animals are capable of 'counting' as adult humans do when they successively label elements with the verbal counting terms 'one,' 'two,' 'three,' etc. to precisely determine the total number of items in a set.

Non-human Animals Represent 'Numbers' Approximately

As alluded to earlier, non-human animals cannot represent numerical values precisely because they lack symbolic language. Symbols such as count words (one, two, three, etc.) or Arabic numerals (1, 2, 3, etc.) are required in order to conceive of precise numerical values because these symbols are discrete representations of the values for which they stand. That is, the Arabic numeral '3,' for example, always represents exactly three items. Non-human animals do not have a symbolic system for representing precise numerical values in this way. Instead of using discrete representations of numerical values, non-human animals represent numerical values approximately, which is akin to estimating. However, it is important to note that, like non-human animals, humans of all ages also represent numerical values approximately even after they learn to count and to use a precise numerical symbol system. Humans therefore possess both a precise and an approximate means of enumerating.

The main behavioral signature of approximate numerical representation is the numerical ratio effect: the ability to psychologically discriminate numerical values depends on the ratio between the values being compared. This effect is known more broadly as Weber's law. An implication of the numerical ratio effect is that there is noise (i.e., error) in the psychological representation of each numerical value that is *proportional* to its value. Hence, larger values are noisier than smaller values. Numerical discriminations that exhibit a numerical ratio effect are approximate discriminations as opposed to precise discriminations because they are noisy.

There is compelling evidence that animals and humans rely on the same system for representing number approximately. When animals and humans are tested in the same nonverbal tasks, their performance is often indistinguishable. In one study, monkeys and adult humans were required to choose one of two arrays that contained the smaller number of elements (**Figure 2(a)**). Humans were instructed to respond rapidly, without verbally counting the elements. When monkeys and humans were tested on identical versions of this numerical comparison task, their patterns of performance were remarkably similar; both groups showed steady decreases in accuracy (**Figure 2(b)**) and increases in response time (**Figure 2(c)**) as the numerical ratio between the stimuli increases. Mathematically speaking, the larger the numerical ratio, the more similar two numerical values are to each other. In this study, as the numerical ratio approached one (a 1:1 ratio in numerical value), monkeys' and humans' performance approached chance accuracy (which was 50%), because the numerical values were too similar to be accurately discriminated by either group at larger ratios.

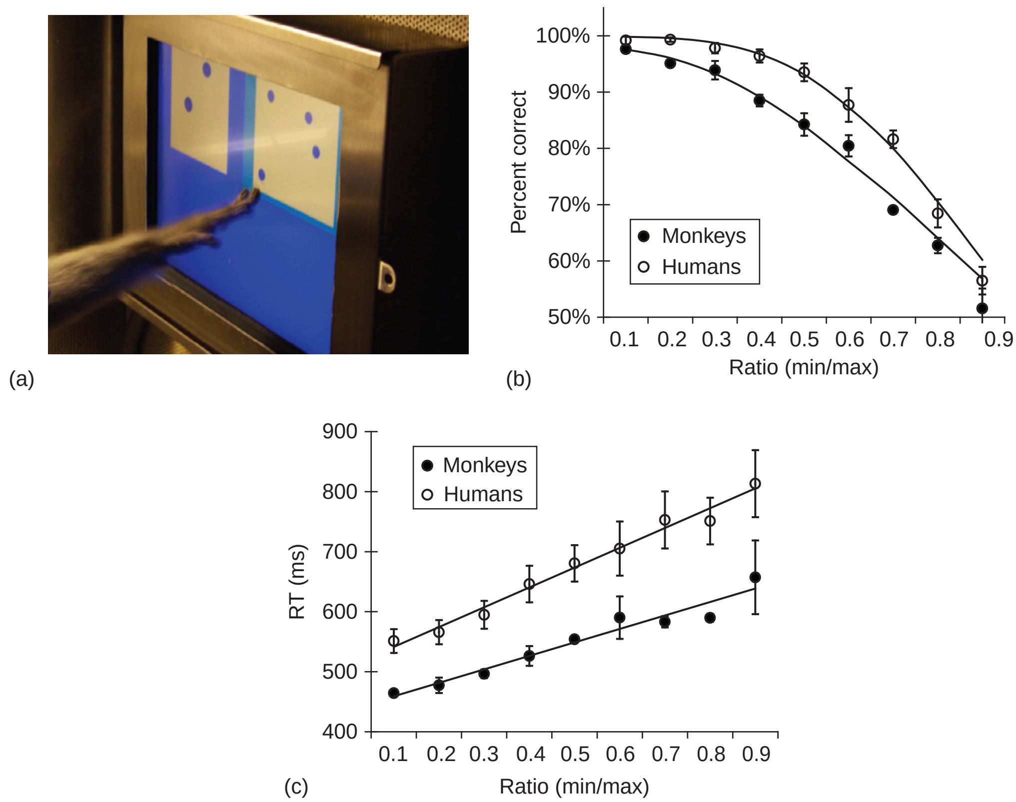

Figure 2 In Cantlon and Brannon (2006), monkeys and humans were given a task in which they had to choose the smaller number of elements from two visual arrays like those in panel (a). Humans were prevented from verbally counting during this task. Monkeys and humans performed very similarly on this task. Both groups performed significantly better than chance (chance = 50%), indicating that they could accurately compare the numbers. For monkeys and humans alike, accuracy decreased (b) and response time increased (c) as a function of the numerical ratio between the two numbers in a given pair (minimum number/maximum number in a given pair). This pattern of performance indicates that for monkeys and humans, numerical comparisons become more difficult as the numerical ratio between values because more similar (i.e., closer to 1 on this scale which represents identical numbers or, a 1:1 ratio in numerical value). Redrawn with permission from Cantlon JF and Brannon EM (2006) Shared system for ordering small and large numbers in monkeys and humans. *Psychological Science* 17(5): 401–406.

Similar parallels between human and non-human animal numerical abilities also have been reported for pigeons and rats on other numerical comparison and estimation tasks. It seems that numerical approximation is a widespread strategy for numerical discrimination throughout the animal kingdom.

A few studies such as those by Tetsuro Matsuzawa and colleagues have shown that animals can use discrete symbols, such as Arabic numerals, to represent numerical values. However, it is important to note that although non-human animals can be trained to associate a symbol with a particular numerical value, this association is not a precise numerical representation in these animals as it is in humans. For instance, macaque monkeys, chimpanzees, and pigeons can be trained to associate the Arabic numerals (e.g., the numerals 1, 2, 3, and 4) with their corresponding values (e.g., sets of 1, 2, 3, and 4 objects). However, after months and even years of training, the animals continue to represent these symbols approximately in that they exhibit a numerical ratio effect in their responses when they match the sets of objects to their symbols. In contrast, adult humans who are given unlimited time to assign an Arabic numeral to a set of objects perform almost perfectly and do not display a numerical ratio effect in their accuracy, because they can verbally count the items to determine the precise numeral that corresponds to the set. Thus, when animals use symbols to compare numerical values, they are limited to approximate numerical representations, whereas adult humans can employ precise numerical representations by counting.

Despite the fact that animals cannot represent precise numerical values as humans do, they can appreciate the ordinal and continuous nature of numerical value. Studies testing animals' abilities to assess relative numerical value (e.g., choose the larger or smaller) have provided evidence that animals understand the ordinal relationships among quantities. There is clear evidence that when trained on one subset of numerical values presented nonsymbolically as arrays of elements (e.g., 1, 2, 3, and 4 elements), monkeys can transfer an ordinal rule (such as ordering from least to greatest) to novel numerical values that are outside that initial training range (e.g., 5, 6, 7, 8, and 9 elements). For example, monkeys trained to order boxes of 1, 2, 3, and 4 dots from least to greatest were able to spontaneously infer that 6 dots is less than 9 dots without being explicitly trained to order sets of 6 and 9 dots. Thus, when comparing quantities, animals appreciate numerical value as a continuum along which values can be ranked from least to greatest.

Ordering is a simple form of arithmetic computation that requires an individual to determine the proximity of a given value to the numerical origin (e.g., zero for humans). Evidence of this simple type of arithmetic ability in non-human animals raises the question of whether they can perform more complex arithmetic operations.

Non-human Animals Mentally Manipulate 'Numbers'

Arithmetic operations, such as addition, subtraction, division, and multiplication, require mental transformations over numerical values. For example, addition is an arithmetic operation that involves mentally combining two or more quantitative representations (addends) to form a new representation (the sum). That is, during addition, an individual has to mentally alter the information it is given (the addends) to create a new representation (the sum). The degree to which animals are capable of mental arithmetic therefore reflects their capacity to mentally transform numerical information.

Many models of foraging behavior assume that animals calculate the rate of return: the ratio of the number of food items or the total amount of food they obtain to the time it took to procure the food. For example, ducks are more likely to congregate around a person throwing bread crumbs at a high rate than a person throwing crumbs at a low rate, showing that they are sensitive to the rate of return of a feeding site. Additionally, great tits (a kind of bird) visit feeding sites in direct proportion to the relative abundance of food at that site (e.g., if a site has food 75% or the time, the birds will visit that site 75% of the time). This probability matching behavior indicates that animals are sensitive to the proportion of instances that an individual feeding site pays off. Such reports predict that animals not only represent 'number' but that they also manipulate numerical representations arithmetically. Indeed, recent studies deliberately testing the arithmetic abilities of animals have confirmed that animals are capable of manipulating their quantitative representations using arithmetic procedures such as addition, subtraction, and proportion (akin to division).

Addition

Several studies have tested animals' abilities to add numerical values together. Moreover, recent studies have begun to test animals' abilities to do mental arithmetic over large and complex ranges of addition problems. For instance, in one study, monkeys and adult humans were presented with two sets of dots on a computer monitor, separated by a delay. After the presentation of these two 'sample sets,' subjects were required to choose between two arrays: one with a number of dots equal to the numerical sum of the two sets and a second, distractor array that contained a different number of dots. The addition problems consisted of addends ranging from 1 to 16, tested in all possible combinations. Monkeys and humans (who were not allowed to verbally count the dots) successfully solved the addition problems, and the two species' accuracy (**Figure 3(a)**) and response times (**Figure 3(b)**) were

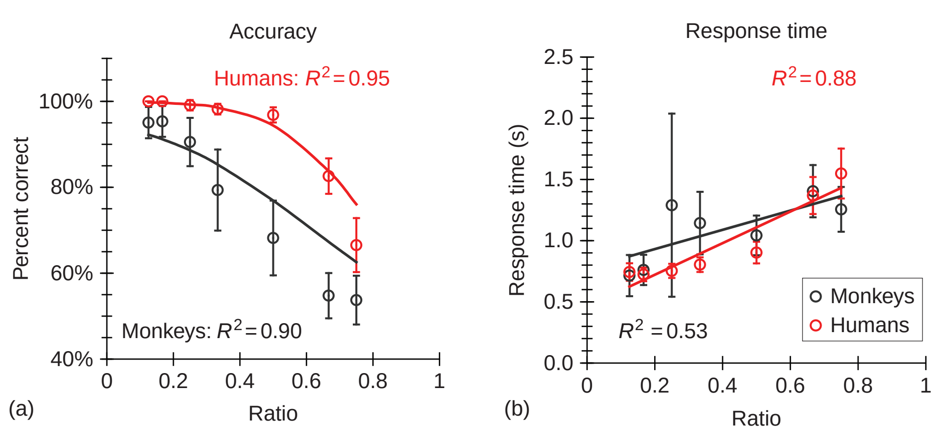

Figure 3 Monkeys and humans were given a task in which they had to add together two sets of dots that appeared successively and then choose the sum from two visual arrays. Humans were prevented from verbally counting during this task. Monkeys and humans performed very well on this task in that both groups performed significantly better than chance (chance = 50%). Moreover, both groups showed the same pattern of difficulty: decreasing accuracy (a) and increasing response time (b) as the numerical ratio between the two choice stimuli increased. Redrawn with permission from Cantlon JF and Brannon EM (2007) Basic math in monkeys and college students. *PLoS Biology* 5(12): e328.

similarly constrained by the numerical ratio between the choice stimuli, or Weber's law. A series of control conditions verified that monkeys' successful performance was not based on simple heuristics such as choosing the array closest to the larger addend. Like humans, monkeys performed approximate addition over the numerical values of the sets.

A series of studies by Michael Beran and colleagues tested non-human primates' abilities to choose adaptively among several food caches containing different amounts of food. These studies have demonstrated that non-human primates can reliably identify the cache containing the largest quantity of food, even when this requires tracking one-by-one additions to multiple caches over long periods of time. Thus, non-human primates are capable of maintaining separate running tallies of different food caches.

Hauser and Spelke have found that monkeys exhibit these kinds of arithmetic abilities even without prior training experience. For instance, when semifree ranging, untrained rhesus monkeys watched as two groups of four lemons were placed behind a screen, they looked longer when the screen was lowered to reveal only four lemons (incorrect outcome) than when the correct outcome of eight lemons was revealed. Monkeys' longer looking time to the incorrect arithmetic outcome can be interpreted as 'surprise.' Thus, as measured by their looking time, monkeys spontaneously form numerical expectations when they view addition-like events and are 'surprised' when an event violates their expectations.

Other studies have trained animals to associate symbols with specific numerical values and then tested the animals' ability to add the symbols. One study showed that pigeons reliably choose the combination of two symbols that indicates the larger amount of food. However, when the number of food items associated with the symbols was varied but total reward value (mass) was held constant, the pigeons failed to determine the numerical sum of the food items, suggesting that they performed the addition task by computing the total reward value represented by the two symbols, rather than by performing numerical arithmetic. Although these data do not demonstrate pure numerical arithmetic in non-human animals, they do indicate that pigeons can mentally combine 'amounts' to choose the larger sum of food. Moreover, this study shows that pigeons can compute total amount abstractly, using symbols to stand for, or represent, the different addends in the problems.

A particularly impressive test of symbolic numerical arithmetic in a non-human animal was conducted on a single chimpanzee by Boysen and Berntson. In this study, a chimpanzee was trained to associate the Arabic numerals 1–4 with their corresponding values. After the chimpanzee was proficient at identifying the value that corresponded to each Arabic numeral (and vice versa), she was tested on her ability to comprehend the arithmetic sum of two Arabic numerals. Sets of oranges were hidden at various sites in a field. Each hidden set of oranges was labeled with two Arabic numerals the sum of which reflected the total number of oranges in the cache. The chimpanzee consistently chose the cache with a combination of Arabic numerals that corresponded to the greatest sum of hidden oranges. Additionally, this chimpanzee was able to view separate sets of oranges and then to identify an Arabic numeral that corresponded to its sum. These experiments demonstrate that non-human animals can use abstract symbols as representations of numerical values to compute approximate arithmetic outcomes.

Subtraction

While there is good evidence that animals can add, evidence that animals can subtract is very scarce. In fact, most studies report that animals struggle to compute the outcomes of subtraction problems. For instance, Hauser and Spelke tested semiwild monkeys' ability to subtract, using the looking time method described earlier that relies on animals looking longer at events that are surprising. In this study, subjects were shown an empty container and then a small number of eggplants were placed inside the container after which the contents of the container were revealed to the subjects. In one condition, two eggplants were placed inside the container, then one eggplant was removed ($2 - 1$ subtraction). When the contents of the box were revealed, the animals either saw one eggplant (not surprising) or two eggplants (surprising). In another condition, one eggplant was placed inside the container and then another was added to the container ($1 + 1$ addition). The contents of the box were revealed just as in the subtraction condition but, in this case, an outcome of one eggplant would be surprising whereas an outcome of two eggplants would be expected.

Monkeys that saw the addition condition looked (appropriately) longer at the unexpected outcome of one eggplant. However, the results were more ambiguous from the subtraction condition: although the majority of monkeys looked longer at the surprising outcome of two eggplants than at the unsurprising outcome, the magnitude of the difference in their looking time between surprising and unsurprising outcomes was not significantly different. One possibility is that monkeys found it significantly more difficult to predict the outcome of the subtraction event than the addition event.

Similar difficulties with subtraction problems relative to addition problems have been reported in chimpanzees. In a study by Michael Beran, chimpanzees watched as food items were added to or removed from two different containers. Then, they were allowed to choose one container to eat its contents. Chimpanzees chose adaptively, maximizing their food intake, when food items were added to containers, but they were less successful when items were subtracted from containers. However, although chimpanzees were not as good at subtractions as they are at additions, they were able to compute some simple subtraction outcomes. For example, when chimpanzees saw one food item removed from a container with anywhere from one to eight food items, they successfully chose the container with more items on the majority of trials. Thus, it was not the case that the chimpanzees failed to understand subtraction operations all together — they just failed to compute problems with large subtracted amounts.

A study by Hauser and Spelke testing the subtraction abilities of wild rhesus monkeys on the same type of subtraction task arrived at a similar conclusion. In that study, monkeys successfully computed the outcomes of simple subtraction problems involving three or fewer total food items but failed on problems involving larger operands. On the basis of these findings, the authors concluded that there might be an upper limit on the magnitude of the subtraction problems that animals naturally compute.

Taken together, findings from subtraction studies suggest that non-human animals are capable of computing subtractions, albeit with limited accuracy relative to addition. However, it may be the case that animals can perform better on subtraction problems in tasks that either do not present the elements of the problems as food items or that test the animals over a wider variety of problems with a more extended task exposure period. Due to the limited number of studies testing subtraction in animals, it is difficult to make a concrete conclusion about animals' capacities for subtraction.

Probabilities and Proportions

A variety of non-human animal species use the proportion and probability of food abundance to guide their feeding choices. Proportion and probability operations are similar to division in the sense that they all require partitioning one quantity as a function of a second quantity to derive a quotient. Two examples of this capacity, discussed earlier, described the use of rate of return and probability matching in foraging birds. These measures are employed not only by birds but can be observed also in the feeding behaviors of many mammalian species. Both the rate of return and probability matching require animals to calculate the total quantity of food divided by the total time foraging. Animals thus appear naturally sensitive to proportions such as rate and probability when these measures factor foraging time and food.

Animals are also capable of computing other forms of proportions. For instance, piranhas seem to use length proportions in order to identify their prey. Piranhas only attack and devour fish that have a 1:4 height–length ratio or greater. The 1:4 proportion rule prevents piranhas from attacking each other, as well as several other types of fish whose height–length ratios fall beneath 1:4. This is a different kind of proportion computation from rate of return and probability matching in the sense that it requires dividing one dimension by a second dimension within the same object.

Laboratory studies, such as those by Nieder and colleagues, have demonstrated that non-human animals can use proportions to reason about problems beyond those they experience in their natural environments. These controlled laboratory studies ensured that animals are truly capable of using 'proportion' to solve problems, rather than using an alternative cue such as absolute size. For instance, a recent study by Vallentin and Nieder showed that monkeys can match sets of lines on the basis of their length proportions.

They trained monkeys to look at a pair of lines, encode the ratio of the length of the first line to the second line, and finally, choose a pair of lines from among a few options that matched the initial pair in length ratio. Thus, if a monkey saw two lines in a 1:4 length ratio on a given trial, they should choose a pair of lines that was also in a 1:4 ratio as opposed to a 2:4, 3:4, or 4:4 ratio. Examples of the length ratios that the monkeys were tested with are shown in Figure 4(a). Importantly, the absolute lengths of the lines were varied such that the animals had to encode the ratio of the lines to arrive at the correct answer; using the absolute length of either or both of the lines would lead to random performance. Monkeys' performance was not random, however, showing that they were capable of basing their matching choices on proportion. In fact, monkeys performed about as well as adult humans who were tested on an identical task (Figure 4(b)). Moreover, monkeys were subsequently tested with novel length ratios (3:8 and 5:8) and showed no decrement in performance on these novel ratios relative to the familiar ratios (1:4, 2:4, 3:4, and 4:4). Broadly speaking, this study demonstrates that monkeys are capable of calculating proportions flexibly, to solve novel tasks testing a range of problems.

Pigeons have been tested in a similar paradigm to this primate study. Jacky Emmerton has tested pigeons' abilities to calculate the proportion of red to green color within horizontal bars and arrays of squares. Half of the pigeons in this study were trained to choose stimuli with a greater proportion of green, whereas the other half chose stimuli with a greater proportion of red. Thus, unlike the previous primate study, this study did not require animals to identify a specific proportion (e.g., 1:4). However, the pigeons' accuracy indicated that they were sensitive to proportion: pigeons were much better at choosing the stimulus with the greater amount of their target color when the proportion was in a greater disparity (e.g., a 1:5 ratio of red to green was easier to discriminate than a 2:5 ratio). Furthermore, a series of control tests revealed that pigeons actually encoded proportion as opposed to absolute amount. Thus, the ability to use proportion flexibly may extend to non-primate and even nonmammalian species.

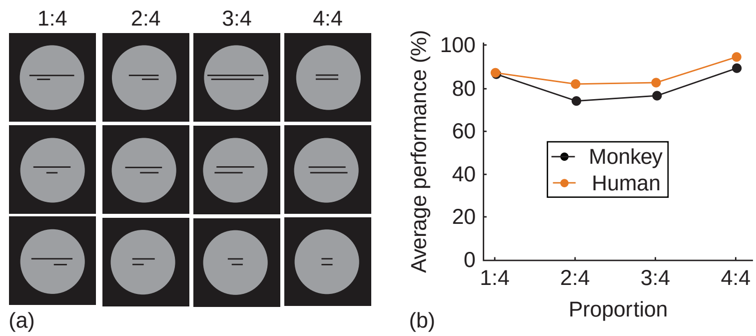

Figure 4 Vallentin and Nieder (2008) tested monkeys and humans on a length proportion matching task in which they had to match the length proportion of two lines to the proportion of another pair of lines (from a series of choices), regardless of the absolute sizes of the lines. As shown in (a), there were four different proportions (1:4, 2:4, 3:4, and 4:4) on which the animals were tested. Different exemplars of each proportion category are shown. Among proportion exemplars, the absolute lengths and positions of the lines vary. Monkeys and humans performed similarly on this task (b) in terms of their overall accuracy and in terms of which proportion categories they found most difficult. Redrawn with permission from Vallentin D and Nieder A (2008) Behavioral and prefrontal representation of spatial proportions in the monkey. *Current Biology* 18(18): 1420–1425.

Several studies have also investigated animals' abilities to make decisions on the basis of the probability of a reward pay-off. Recently, Yang and Shadlen demonstrated that monkeys are even capable of adding probabilities together to determine their sum. In this study, monkeys were shown different shapes that were each associated with a specific probability that one of two choice targets (a red circle or a green circle) would pay-off a reward (fruit juice). On each trial, the monkeys had to look at a shape and then choose either the red target or the green target. There were ten possible shapes whose probabilities of pay-off ranged from a 100% chance that the red target would pay off to a 100% chance that the green target would pay off. So, for example, a monkey might see a shape associated with a 70% chance that the red target would pay off and, in this case, he should choose the red target as opposed to the green target. Once the monkeys learned to choose targets appropriately on the basis of the probability of pay-off associated with each of the ten shapes, they were given a more complicated task.

In the more complicated version of the task, the monkeys were shown a combination of four shapes and were required to choose a target on the basis of the sum of the probabilities of the four shapes (**Figure 5**). For example, a monkey might see a shape associated with a 70% chance of red paying off, a second shape with a 90% chance of green paying off, a third shape with a 70% chance of green paying off, and a fourth shape with a 70% chance of red paying off. In this example, the sum of these probabilities results in a 20% chance that green will pay off and the monkey should choose the green target. This example is shown in **Figure 5**.

Across many trials, with many different combinations of shapes, the monkeys chose the correct target on the majority of trials on the basis of the cumulative probability of the shape combination. Of course, the monkeys computed these probabilities only approximately and thus, they made errors when the difference between the sum of the red- and green-target pay-off probabilities was slight. However, it is impressive that monkeys chose the appropriate target on the majority of trials, given that 715 different combinations of shapes were tested. This large number of possible shape combinations would have made it impossible for the animals to learn or memorize the pay-off probabilities of the combined shapes. The animals therefore had to compute the sum of the probabilities across the four shapes to choose

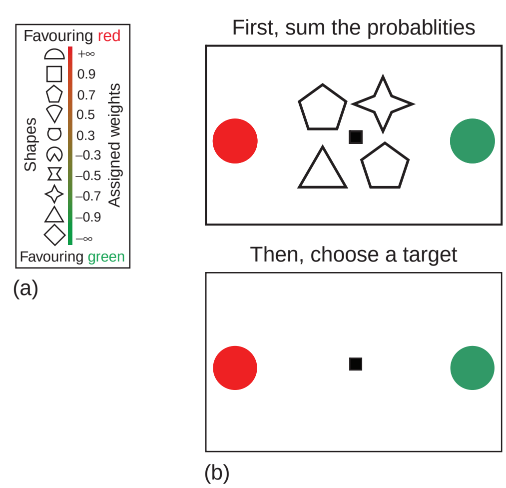

Figure 5 Each shape in panel (a) is associated with a probability that the red or green target will pay-off a juice reward. Monkeys were shown four shapes on a computer screen, and then they were required to choose either the red or green target (b). In order to choose the correct target, monkeys had to compute the probability that the red or a green target would pay-off by summing the probabilities from these four shapes for favoring the two targets. Using the scale in panel (a), the sum of the four shapes in panel (b) indicates that there is a 0.2 probability that the green target will pay-off and so, the monkey should choose the green target (Yang and Shadlen, 2007). Redrawn with permission from Yang T and Shadlen MN (2007) Probabilistic reasoning by neurons. *Nature* 447(7148): 1075–1080.

the appropriate target; this is analogous to performing a computation (addition) on a computation (probability). Evidence that non-human animals can compute complex calculations such as these raises the possibility that their minds are capable of computing a whole host of approximate arithmetic computations.

Conclusion

Quantitative thinking appears to be an inherent aspect of decision-making throughout the animal kingdom. Studies of the behavior of animals in their natural habitats and during controlled laboratory tasks have revealed a level of arithmetic sophistication in non-human animals that once may have been considered uniquely human. So far, there is evidence that animals can add, subtract, estimate a proportion or probability, and add probabilities. Unlike humans, non-human animals are limited to entering approximate quantitative representations into these operations. However, regardless of differences in the precision of human and animal representations, approximate arithmetic operations seem to function quite similarly in humans and other animals. Humans and non-human animals perform at comparable levels of accuracy on arithmetic tasks that force humans to use approximate numerical representations by preventing them from verbally counting or labeling units.

The parallels in human and non-human animal approximate arithmetic suggest an evolutionary link in their quantitative capacities. That is, the types of quantitative abilities described herein likely have been around for millions of years. Moreover, evidence of non-human animal arithmetic advances the hypothesis that quantitative reasoning is a component of a primitive cognitive system that exists even without language. Animals that do not use symbolic language to express their thoughts nonetheless possess the ability to perform arithmetic and quantitative computations. Together, these findings underscore the existence of extraordinary continuity in the thought processes of humans and other animals, despite the obvious differences between them.
The parallels in human and non-human

Although we have discussed some broad similarities in the quantitative capabilities of many animal species, the degree to which species subtly differ in their arithmetic abilities remains to be explored. For instance, animal species that naturally reason about length proportions in their environments (e.g., piranhas) may solve length proportion tasks more easily than species that do not. Studies that compare arithmetic capacities between species using comparable tasks are needed to address such questions. Additionally, in order to develop specific hypotheses for revealing differences among species, the degree to which animals face quantitative problems and use quantitative strategies in their natural environments needs to be explored in greater detail. This type of research would help to further delineate the evolutionary relationships among the quantitative abilities of different animal classes.

See also: Categories and Concepts: Language-Related Competences in Non-Linguistic Species; Cognitive Development in Chimpanzees; Time: What Animals Know.

Further Reading

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