Monkeys, coots, salamanders and even bees can count. But why did numeracy first evolve?
CLEVER HANS's gift was just too good to be true. The Arabian stallion wowed the crowds in early 20th-century Europe with his apparent ability to stomp out the answers to simple mathematical problems, such as $12-3=9$. He could even add fractions and factorise small numbers. Then in 1907, a German psychologist, Oskar Pfungst, proved that Hans was no animal savant.
In a scientific trial of sorts, Pfungst demonstrated that Hans could do arithmetic only when his owner, a maths teacher, or another questioner provided unconscious body cues hinting that Hans had reached the correct answer. With blinkers on or with the questioner hidden, Hans's abilities vanished. So, too, did the notion that animals could count.
Much has changed, however, in the century since Clever Hans's ignominious exposure. Few now doubt that primates have a sense of number, and even distantly related animals, including salamanders, honeybees and newly hatched chicks, seem to have the knack, with some able to perform basic arithmetic. What's more, the skills of this growing mathematical menagerie resemble our own innate abilities. Could basic mathematics have evolved hundreds of millions of years ago?
"The ability to represent time and space and number is a precondition for having any experience whatsoever," says Randy Gallistel, a psychologist at Rutgers University in Piscataway, New Jersey.
Of course, without language or a precise symbolic system to represent numbers, animal numerical abilities will never reach human levels. No chimpanzee will ever learn long division, but with enough practice almost any human can master the challenge. So to put humans and animals on an equal footing, we need to look at more basic numerical faculties. Prime among those is the ability to distinguish between a larger and a smaller number, says Elizabeth Brannon, a psychologist at Duke University in Durham, North Carolina. Humans can do this with ease - providing the ratio is big enough - but do other animals share this ability?
In one experiment, rhesus monkeys and university students had to choose the bigger of two sets of geometrical objects that appeared briefly on a computer monitor. Both groups performed successfully. Importantly, Brannon's team found that monkeys, like humans, make more errors when the ratio between the two groups is smaller. "The students' performance ends up looking just like a monkey's. It's practically indistinguishable," she says.
This ancient cognitive capacity even seems to dictate the way we humans understand written numbers. When asked to determine which of two Arabic numerals is larger, a person's reaction time increases as the ratio between the two numbers decreases: it takes someone longer to recognise that 10 is larger than 9, than that 10 is larger then 5 (Current Opinion in Neurobiology, vol 16, p 222).

## Greedy salamanders

Primates are not the only animals whose numerical capacities rely on ratio, however. While at the University of Louisiana in Lafayette, Claudia Uller, a psychologist now at the University of Essex in the UK, wondered whether our more distant relatives could also distinguish large numbers from small.
To investigate, her team tempted local red-backed salamanders (Plethodon cinereus) with two sets of fruit flies held in clear tubes. In a series of trials, the researchers noted which tube the amphibians scampered towards, reasoning that if they had a capacity to recognise number, they would head for the larger number of tasty snacks.
At rates well above chance, the salamanders successfully discriminated between tubes containing 8 and 16 flies, for example, but not between 3 and 4, 4 and 6 , and 8 and 12 (Animal Cognition, vol 6, p 105). So it seems that for the salamanders to discriminate between two big numbers, the largest must be at least twice as big as the smallest.
That was not the case, however, for numbers up to and including 3 . The salamanders could differentiate between 2 and 3 flies just as well as 1 and 2 flies, suggesting they recognise small numbers in a different way to larger numbers. This chimes with studies showing that adults, infants and primates can also differentiate precisely between small numbers, irrespective of the ratios between the quantities.
Together, the results suggest that the two abilities - to precisely identify small numbers and to estimate the relative size of large numbers - have deep roots in our evolutionary history. "There's a good chance that this thing goes way back," says Marc Hauser, a psychologist at Harvard University, who has led many of the primate studies.
Further support for this theory comes from studies of mosquitofish (Gambusia holbrooki), a freshwater species native to the south-eastern US which instinctively join the biggest shoal they can. A team led by Christian Agrillo at the University of Padua, Italy, found that while lab-reared fish can tell the difference between 3 and 4 shoal-mates, they did not show a preference between 4 and 5 of their brethren. Agrillo's team also found that mosquitofish can discriminate between numbers up to 16 , but only if the ratio between the fish in each shoal was greater than $2: 1$. This indicates that the fish, like salamanders, possess both the approximate and precise number systems found in more intelligent animals such as infant humans and other primates (Animal Cognition, vol 11, p 495).
While these findings are highly suggestive, some critics argue that the animals might be relying on other factors to complete the tasks, without considering the number itself.
"Any study that's claiming an animal is capable of representing number should be controlling for surface area, density and perimeter," says Brannon. Experiments have confirmed that primates can indeed perform their numerical feats without these clues, but what about the more primitive animals?
To consider this possibility, Agrillo repeated his mosquitofish tests, this time using geometrical shapes of varying size and brightness in place of their shoal-mates. Using these shapes, the team arranged the two "shoals" so that they had the same overall surface area and luminance even though they contained a different number of objects.
Across hundreds of trials on 14 different fish, Agrillo's team found they consistently discriminated 2 from 3 (PLoS ONE, vol 4, e4786). He is now testing whether mosquitofish can also distinguish 3 geometric objects from 4, without volumetric cues.
This ability may date back to even more primitive organisms than fish. Jürgen Tautz, an entomologist at the University of Würzburg in Germany and colleagues sent a group of bees down a corridor, at the end of which lay two chambers one with a sugar water reward, the other with nothing. To test the bees' numeracy, the team marked each chamber with a "room number" consisting of 2 to 6 shapes. A similar sign at the beginning of the corridor indicated which room would contain the reward. Like Agrillo, the team accounted for geometric aspects that might have given the game away. Nonetheless, the bees quickly learned to match the number at the entrance with the correct room number. Like the salamanders and fish, there was a limit to the bees' mathematical prowess - they could differentiate up to 4 shapes, but failed with 5 or 6 shapes (PLoS ONE, vol 4, e4263).
So it seems that even our most distant relatives have some concept of number, but these studies still don't show whether animals learn to count through training, or whether they are born with the skills already intact. If the latter is true, it would suggest there was a strong evolutionary advantage to a mathematical mind.
Proof that this may be the case has emerged from an experiment testing the mathematical ability of three and four-dayold chicks. Like mosquitofish, chicks prefer to be around as many of their siblings as possible, so they will always head towards a larger number of their kin. They, too, have very low standards for what constitutes a sibling; if chicks spend their first few days surrounded by small balls or scraps of paper, they become attached to these inanimate objects as if they were family.
Rosa Rugani and Lucia Regolin at the University of Padua took advantage of this quirk to test whether chicks could perform simple calculations. They placed each chick in the middle of a platform and showed it two groups of balls or paper. Next, the researchers hid the two piles behind screens, and sequentially moved objects between them in view of the chick. This forced the chick to perform simple computations to decide which side now contained the biggest number of its newfound brethren (Proceedings of the Royal Society B, vol 276, p 2451).
Without any prior coaching, the chicks scuttled to the larger quantity at a rate well above chance, correctly determining that $1+2$ was greater than $4-2$, that $0+3$ exceeded $5-3$, and that $4-1$ was more than $1+1$. "They are doing some simple, very simple, arithmetic," Regolin says. This suggests that numeracy is an innate ability in many animals that does not require training.
Why these skills evolved is not hard to imagine, since it would help almost any animal forage for food, says Gallistel. Animals on the prowl for sustenance must constantly decide which tree has the most fruit, or which patch of flowers will contain the most nectar.
There are also other, less obvious, advantages of numeracy. In one compelling example, Bruce Lyon of the University of California in Santa Cruz found that female American coots appear to count their eggs - and those in the nest laid by intruders - before making any decisions about increasing their clutch size (Nature, vol 422, p 495).
Exactly how ancient these skills are is difficult to determine, however. Just because bees, salamanders, fish and humans share similarities in their ability to detect number, it does not necessarily mean they all inherited the talent from a common ancestor.
Numerical ability might just emerge in any sufficiently advanced nervous system faced with an environment in which numeracy would prove an advantage, says Tautz. Just as bat and bird wings evolved separately yet work using the same fundamental principles, numerical representation may have developed in many separate instances. Brannon agrees: "We clearly must be talking about convergent evolution or something that is so primal that it traces back to millions and millions of years ago."
Unlike bony wings, number-crunching brains leave little trace in the fossil record. Only by studying the numerical abilities of more and more creatures using standardised procedures can we hope to understand the basic preconditions for the evolution of number.
Working towards that end, Uller and her team have now returned horses to the counting club. In work to be published in Animal Cognition, Uller found they can distinguish 2 apples from 1, 3 from 2, and 6 from 4 (DOI: 10.1007/s10071-009-0225-0). And when presented with two smaller apples similar in volume to one larger apple, horses still go for the larger number. Her experiments are not a validation of Clever Hans and his believers, but they might do something to restore his good name.

By Ewen Callaway

