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Animals do count

Research sheds light on the evolution of numerosity across the animal kingdom

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The ability to count and perform simple numerical calculations is not confined to *Homo sapiens* but is, in fact, widespread across the animal kingdom, with wide variations in capability that reflect evolutionary drivers almost as much as brain capacity. Recent advances have started to elucidate not just the capabilities themselves but also the neural correlates and selective advantages. It seems that a basic underlying numerosity, that is, a facility for estimating and comparing quantities of objects or events, is innate in many animals, and that it has evolved independently across different taxa. Understanding the detailed mechanics of operation, or the algorithms used, can shed light on the ingenuity of nature to solve surprisingly complex problems, and even suggest new problem-solving approaches for humans.

How frogs and bees count

Many recent advances are covered in a book entitled *Can Fish Count?* by Brian Butterworth, a cognitive neuroscientist at University College London, published in March 2022. Butterworth argued that a basic sense for number is hardwired in most if not all animals, but that it is refined during life to varying degrees through the animal's experience. Such exposure can take many forms through incorporation of multi-modal sensory inputs with memory informing decisions that lead to outcomes that may involve fleeing, attacking, or hiding. Most inputs for numerosity are visual, but acoustic and even tactile inputs are also involved.

Numerosity relating to acoustic input is common among anurans, the order of amphibians that includes frogs and toads, and it is related to reproductive behaviour. Males issue several types of call, which can increase in complexity during aggressive interactions between males, or when they are approached by females. In such situations, males have been found to match their neighbours in the number of calls they make and the intervals between then, which reveals some numerical abilities even if just in counting. Furthermore, neural correlates have been found in the form of "interval-counting" neurons, which can be tuned to fast pulse rates and that respond only when a threshold number of pulses has occurred within the correct timeframe. When such an interpulse interval is say two or more times the optimal value, the whole counting process is reset and starts again (Rose, 2017).

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The author made whole-cell recordings from midbrain neurons *in vivo* which revealed that the call-matching process was associated with a complex interplay between activity-dependent nerve-cell excitation and inhibition. Single pulses primarily elicited inhibition but, as additional pulses were presented at optimal intervals, cells become progressively depolarized and spike after a threshold number of intervals. This process appears to involve a combination of innate capabilities associated with these specialized interval-counting neurons, and training through experience to tune to the required intervals.

Similar combinations of basic innate sense and subsequent refinement have been studied in a growing number of other animals, notably bees (*Apis mellifera*), which count landmarks along their routes to help navigate between hives and plants where they gather nectar (Chittka & Geiger, 1995). In this early study, bees were trained along a row of four identical landmarks in an area 300 m long, comprising equally spaced tetrahedral tents with a feeding source placed between the third and fourth landmark. The authors altered the number of tents between hive and feeder between experiments and found that the bees flew further the greater the distances apart, but always passed the same number of landmarks. This was taken as evidence that the bees rely on counting these landmarks for navigation, particularly perhaps for return visits to plants with plenty of nectar remaining to be harvested.

This early work spawned further research leading to the recent understanding that bees have evolved a simple sequential approach to counting that is optimized for their limited brain capacity. Bees have less than 1 million neurons, compared with 86 billion for humans, which prevents them from complex visual analysis to assimilate whole scenes at a glance. Instead, they confine their counting to small sets of distinct objects in sequence, which can be coded more efficiently and is sufficient for navigating in a local area. A recent study explored this hypothesis that bees are unable to rely on a single sensory snapshot to make numerical discriminations and instead enumerate small sets of items through sequential scanning one after the other (MaBouDi *et al*, 2020). The implication is that the time taken to make number-based visual

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discriminations depends on the set sizes to be enumerated, which appears to be the case.

The concept of zero

Yet, despite these limitations, bees appear at some level to have two astonishingly advanced capabilities: they have a concept of zero as a value and they are able to address the famous travelling salesperson problem, which involves finding the shortest possible distance required to visit a given set of locations.

At first sight, it seems remarkable that animals should have an understanding of zero at all since say the absence of predators or food sources would seem to be quite distinct from the presence of them when counting might provide an advantage. But there are contexts where the value zero is just part of the numerical continuum, and that seems to be how animals regard it as far as research can tell. A 2021 study at the University of Tübingen in Germany analysed the behavioural and neuronal representation of the value zero in crows, which have considerably greater cognitive capabilities in most senses than bees (Kirschhock *et al*, 2021). The authors showed that crows can grasp an empty set as a null numerical quantity mentally represented next to number one and that single neurons in an associative cerebral region respond to it specifically with the same physiological characteristics as countable quantities. The study also found that crows confuse the value 1 more often with zero than they do the value 2 and even more so three. For them, zero is at the bottom of the number line, rather than a distinct concept.

Bees share this ability to represent zero, according to an Australian study that trained individuals to compare groups on the basis of greater or less than (Howard *et al*, 2018). Bees were able to extrapolate the concept of less/greater than to zero as being smaller than 1, in a way comparable to other animals where this has been observed, including the African grey parrot, nonhuman primates, and even preschool children, according to the authors. "Our research showed that honeybees could perform quantity discrimination of 1–10 items with extensive training, discrimination being coarser without training, learn the relational rules of greater versus lesser, order zero in the correct position among the quantities 1–6, perform simple arithmetic of adding or subtracting one from a set of items, match abstract characters to quantities to yield symbolic representation of number, and finally, learn to categorise quantities 1–10 by parity, that is odd or even categorization, and apply this to the novel quantities of 11 and 12," explained Scarlett Howard, Head of the Integrative Cognition, Ecology and Bio-inspiration (ICEB) Research Group at Monash University in Australia and a lead author on that paper.

That is quite a list and maybe unique among insects or invertebrates generally, given the specific pressures on bees to collect nectar. Certainly, the numerosity of bees has been widely studied because of their trainability, according to Adrian Dyer, an animal vision specialist at rMIT University in Australia. "Still very little is known in a comparative sense between bees and other insects," Dyer said. "We are fortunate that bees respond well to learning experiments, but this is not the case for many other insects, so it is hard to know complete answers. There is however some work in fruit flies that might suggest a basis for common links. However, bees are prolific foragers so this might promote their capacity, but there is much still to learn."

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Solving algorithmic problems

One other capability of bees is their ability to solve, or at least tackle, the travelling salesperson problem. This is an algorithmic problem designed to find the shortest total distance when visiting a specified group of locations and arose in the traditional context of a travelling salesperson visiting a given number of clients or prospects. The problem is equally relevant to a bee seeking to gather as much nectar as possible for the least flying distance so as to save energy in the process.

The ability of bees to traverse routes comprising multiple destinations with increasing efficiency was assessed in a study using harmonic radar to track a group of the insects around an array of five artificial flowers deliberately arranged such that attempts by bees to reduce travel distances between individual feeders would fail to minimize the overall distance travelled. This avoided concluding falsely that bees were optimizing their overall distance when they were merely taking the shortest distance between the artificial flowers (Woodgate *et al*, 2017). Harmonic radar technology has been widely used for tracking insects via tiny tags which use the original radio signal as its energy source and re-emit it as a harmonic of the original, thereby providing information on location and speed.

The bees tended to repeat the same journey, visiting the same feeders, but gradually reduced the distance by flying in straighter lines between them. It did not appear they changed the order with which they visited the feeders, as might be necessary to determine the shortest total route possible, but this may have been beyond their cognitive capabilities. Nonetheless, this and other studies of bees have shown that quite advanced numerosity can be achieved with relatively small neuronal structures when selective forces are strong enough.

Obviously, selection for numerosity – in the sense of distinguishing between numbers of objects and events rather than just assessing properties such as size and density as continuously varying quantities – is quite strong for many animals. "It seems that numerical discrimination of an approximate type such as that associated with Weber Law is useful in a variety of contexts, prey and predatory behaviours, foraging, mate choice and so on," commented Giorgio Vallortigara, Professor of Neuroscience at the University of Trento in Italy. "What is striking is the evidence that 'pure' discrete numerousness is used by animals, that is that computations are done using numerosities and not the continuous physical variables that in stimuli co-vary with number, such as size, contour length, and density. This suggests that it could be useful for animals to possess some sort of 'general currency' for estimation of quantity for performing the equivalent of arithmetic operations, and in fact there is evidence that the number sense allows animals to perform arithmetic." Weber's Law as cited by Vallortigara states that the increase in a quantity required to be discernible by the brain is proportional to the baseline, implying that numerosity perception is logarithmic rather than linear. In other words, animals discern the difference between 2 and 4 as being the same as between 1 and 2, rather than 0 and 2 as would be the case using merely the gap between numbers as the measure.

The evolution of numerosity

The widespread existence of numerosity among animals raises the question whether it derives from highly conserved processes or genes, or arose many times because of convergent evolution, or some combination of the two. "The knowledge that similar numerical abilities are observed in, or can be taught to, a range of animals suggests two evolutionary processes," Howard mused. "One option is that a 'sense of number' is evolutionarily conserved, originally appearing in a common ancestor which had evolved it from necessity. The other option is that number sense has evolved multiple times in animals with very different brain structures and architectures, as we see it in taxa as diverse as mammals, birds, fish, reptiles, amphibians, and insects. Parallel evolution would suggest that there is a strong enough need in different environments and scenarios for different species to evolve and retain a capacity to process numerical information. There still seems to be debate in the field as to whether there is enough evidence to support one theory over the other."

"Some results seem to suggest homoplasy, that is convergent evolution," Vallortigara agreed. "For instance, in crows the number neurons have been described in the NCL (nidopallium caudolaterale) that is considered analogous of the mammalian prefrontal cortex, but not homologous, that is evolved from common ancestry. Also, the fact that invertebrates possess similar behavioural mechanisms might suggest parallel evolution under similar selective pressures. On the other hand, it is striking that the same signatures are observed in all taxonomic groups, that is distance and size effects in numerousness discrimination that show that discrimination always obeys Weber's Law." The nidopallium, meaning nested pallium, is the region of the avian brain used both for some executive functions and higher cognitive tasks. It is subdivided into smaller regions one of which, the nidopallium caudolaterale, is believed to carry out many of the complex, higher order cognitive functions in birds (Atoji & Wild, 2009).

The human condition

Research into animal numerosity has obvious relevance for the study of cognitive evolution, but the work identifying neural correlates and underlying genes could also have direct benefits for humans, particularly those who have difficulties with numbers. A significant number of people, estimated at between 3% and 6% among school-age children (Shalev *et al*, 2000), suffer from dyscalculia, a deficit in numerical abilities analogous to dyslexia. Sufferers are often deficient not just in mental arithmetic, finding difficulty counting backwards for example, but tend to have a poor sense of estimation, trouble judging distances, clumsiness, and even accident proneness, which affects their quality of life. Dyscalculia may well also be related genetically to other conditions relating to cognition, learning difficulties, and concentration, such as autism and dyslexia.

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Following progress unravelling the neurological and genetic underpinnings of numerosity, research is now starting to focus on dyscalculia, Vallortigara commented. "This is in fact one of the main goals of a project we are currently developing with Caroline Brennan of Queen Mary University in London, Scott Fraser at the University of Southern California, and Brian Butterworth from UCL London, studying in zebrafish some candidate genes for human dyscalculia," he said. This will involve examination of larval zebrafish brains using light sheet microscopy and imaging, Vallortigara added. "Finally, on a more cognitive side, we are planning to explore more sophisticated numerical tasks using archerfish and in young chicks we are looking for the presence of number neurons at the onset of life."

There is evidence that dyscalculia is highly heritable (Shalev *et al*, 2001), but identifying specific genes has so far proved elusive. Currently therapies are limited to alleviating associated conditions such as ADHD or anxiety, which can then help reduce the deficits, but identifying specific genes, or neural correlates, would open the door to new advanced therapies. In that regard, a better understanding of how numerosity evolved and how it works at the neuronal level across many species could greatly benefit research on human's more sophisticated arithmetic capabilities and not just on how to help patients suffering from dyscalculia.

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