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Introduction

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Introduction: The origins of numerical abilities

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1. Introduction

The papers in this theme issue are based on a discussion meeting at Royal Society in London on 20 and 21 February 2017, and at their Kavli Centre at Chicheley Hall in Buckinghamshire on the 22 and 23 February. In addition to the scientific presentations, two distinguished mathematicians, Fields Medallist, Cédric Villani and Professor of Mathematics at Oxford University, Marcus du Sautoy, summed up the implications of our new understanding of the origins of numerical abilities for mathematics and for mathematics education. Audio recordings of the talks and the subsequent discussions can be accessed at https://royalsociety.org/science-events-and-lectures/2017/02/numerical-abilities/, https://royalsociety.org/science-events-and-lectures/2017/02/numerical-abilities-future/.

It is clear that humans have a sense of number. This is evident from their ability to count using counting words, such as one, two, three, . . . and counting symbols, such as 1, 2, 3, . . . or I, II, III, IV, ... In fact, Pagel & Meade [1] argue that reconstructions of the deep history of cognates from diverse language families show that counting words are among the longest-surviving words in all languages. Even when the culture fails to provide words or symbols to notate counting, humans are still able to enumerate objects in their environment, as evidence from work with Australian Aboriginal children [2], suggesting that the symbolic forms, perhaps especially the number words, arose to denote a pre-existing concept of number.

One of the oldest questions in Western philosophy is what is a number that we may have a sense of it. Giaquinto [3], in his paper in this issue, notes that Euclid defined a number as 'a multitude of units' where a unit is a single individual thing. According to this view, 'any pair of items is a 2 and so there are many 2 s; any trio is a 3 and so there are many 3 s. In general, any plurality of k things is a k and there are many ks'. Given that there are many twos, the immediate problem is that we might recognize a brace of pheasants and Big Ben striking two, but how do we know they are the same number? This kind of epistemological problem exercised Plato, though he was more concerned with geometrical forms than numbers.

These accounts are consistent with the widely held view that our numerical abilities—even the ability to recognize and discriminate particular numerosities (the number of objects in a set)—depends on the power of human reason to construct numbers in a kind of logical way. This view has been promoted very influentially by Piaget [4] and by Howard Gardner, for whom one 'intelligence' was 'logico-mathematical' [5]. Thus, the philosopher and mathematician, Bertrand Russell wrote in 1919, 'It must have required many ages to discover that a brace of pheasants and a couple of days were both instances of the number 2: the degree of abstraction involved is far from easy' [6, p. 3].

However, at least 80 years ago carefully controlled experiments with crows and ravens demonstrated that these creatures, which did not have the advantage of relevant culture, and perhaps not of the relevant human reasoning capacities, were nevertheless able to carry out simple numerical tasks successfully showing that they too had a sense of number [7]. Using a match to sample paradigm where non-numerical dimensions—such total surface area of the objects, total length of edges, etc. were randomly varied—it was shown that these birds were able to make matches reliably up to seven items.

This raises the question of how we and other creatures have a sense of number. Evidence from bones and stones shows that Homo sapiens had a sense of number, as d'Errico [8] describes in great detail, tracing the prehistoric development of numerical notation from incidental notches arising from butchering animals to systematic and intentional marks not only on bones but also in other media. Jacobs Danan & Gelman consider how children develop and refine their sense of number, and make contact with the cultural tools available to them, in particular, the difficult transition from whole numbers to fractions and decimals [9].

2. The phylogenetic ubiquity of the number sense

Half a century ago, the assumption that the ability to perceive and reason about number was uniquely human was taken more or less for granted in all of the cognitive sciences, Koehler's above-mentioned evidence to the contrary notwithstanding. Experimental work in the last several decades has essentially reversed that assumption. There is now a broad consensus that the perception of numerosity and elementary numerical computation (the application of the ordering operation, $\geq$, for example) to number percepts are found even in arthropods. The arthropods diverged from the chordata (hence from the later evolving vertebrata and mammalia) in the early Cambrian.

The numerical ability of different species will depend on its adaptive value. In small fish, such as guppies, an individual fish is safer from predation when it is in a shoal, and the larger the shoal the safer it is, other thing being equal. So being able to assess and compare the number of fish in a shoal is valuable, as Agrillo & Bisazza [10] demonstrate. In their review of the experimental evidence, they emphasize the similarity of these findings to those obtained from mammals, including humans. They show that when comparing two numerosities, like comparing other quantities—such as size, weight, luminance—non-human minds obey Weber's Law, which is the oldest and most broadly applicable quantitative law in experimental psychology. It says that the discriminability of two quantities—the speed and accuracy with which the larger of the two can be decided on—depends only on the ratio of the two objectively specified quantities. Thus, for example, the speed and accuracy with which a 6 g weight can be distinguished from a 4 g weight are the same as the speed and accuracy with which a 6 kg weight can be distinguished from a 4 kg weight. Similarly, the speed and accuracy with which a set with numerosity of 6 can be distinguished from a set with numerosity 4 are the same as the speed and accuracy with which a numerosity of 60 can be discriminated form a numerosity of 40. The dependence of discriminability solely on the objectively measured ratio has two consequences called the size effect and the distance effect. The size effect refers to the fact that the discriminability of given numerical difference depends on the size of the two discriminanda. Thus, for example, a difference of 2 is easily recognized when the discriminanda are 4 and 2, but the same difference is unrecognizable by the non-verbal system for representing numerosity when the discriminanda are 52 and 50. The distance effect refers to the fact that the discriminability of two numerosities depends on how widely separated they are. We—and all other vertebrate species tested—more readily discriminate 10 from five than we discriminate six from five. Both the size effect and the distance effect are implied by Weber's Law. This property of the non-verbal representation leads to its being called the Approximate Number System. Remarkably, this Weber's Law property also governs the reaction times of human subjects when deciding on the ordering of two numerals (the written symbols for number) [11,12].

Male frogs, and other anurans, use enumeration for a quite different purpose, as Rose describes [13]. The number and type of calls is an advertisement to neighbouring, and (usually invisible) conspecific females. Because females prefer longer and more complex calls, males try to include more 'chucks' (brief, harmonically rich notes) than their competitors. 'To match or '1-up' their competitors, male tungara frogs can add up to 4–6 chucks to their advertisement calls, thereby showing evidence of counting to at least this number'.

For a honeybee, it turns out to be useful to count landmarks to assess distance between a food source it has found and its hive. It may also useful to count the number of petals on flower as a way of identifying a good food source, as Skorupski *et al.* [14] note. However, whether the bees' system obeys Weber's Law for large numerosities has yet to be proved in invertebrates, though for non-countable quantity (i.e. continuous rather than discrete quantities) Weber's Law applies also to invertebrates.

Many social mammals in the wild, African lions, spotted hyenas and wolves, assess the number of conspecifics calling and respond based on numerical advantage, as Benson-Amram *et al.* [15] show. One adaptive advantage of doing this is to decide between fight or flight if outnumbered. Comparisons of their own group number with that of a competing group broadly follow Weber's Law.

Nieder [16] shows that both rhesus macaques and corvids recognize specific numerosities using a match-to-sample paradigm very similar to the one pioneered by Koehler, with performance showing Weber-like properties.

Studies of day-old chicks (*Gallus gallus*) by Rugani [17] and colleagues show that they can discriminate between different numbers of objects in Weber-like manner, can solve rudimentary addition and subtraction problem, and use ordinal information to identify a target element, (e.g. fourth from the left). This is an elaboration of the well-known imprinting mechanism in which the chick follows the first moving object it sees. Approaching more rather than fewer nest-mates provides better protection against predation and less heat dissipation.

Numbers are intimately related to space. For example, human children typically learn to count objects distributed in space, and the sequence of digits on school walls and in books is a spatial sequence, usually with the numbers ascending from left to right. Is this why humans typically show an advantage in tasks where leftward responses are quicker for low numbers than high numbers (the spatial-numerical association of response codes, or 'SNARC' effect [18]? This evidence has been taken to suggest that we possess a 'mental number line' in our heads, oriented left-to-right. We may ask why numerate cultures prefer this left to right organization. Vallortigara [19] explores its evolutionary origin in the preference of chicks for low numerosities to be on the left, and to carry out an ordinal count (e.g. fourth from the end) more readily if the end is on the left.

3. The neurobiology of numerical abilities

Neuroimaging studies have revealed a network comprising three main linked cortical regions that are almost invariably activated in any number task: the parietal lobes bilaterally, particularly the intraparietal sulcus, and the left frontal lobe [20–22]. Butterworth [2] reports evidence that the development of the parietal lobes is markedly atypical in learners with dyscalculia, a congenital disability in learning about numbers and arithmetic; moreover, evidence from twins suggests that in some cases of dyscalculia, the neural abnormality is inherited. These parietal regions support more than simple numerical tasks; Amalric & Dehaene [23] show that they are 'recycled' by professional mathematicians doing advanced mathematical tasks, and that the neural basis of memory for mathematical material—facts and formulae—is distinct from language-based memories.

Nevertheless, many studies over the past 100 years have found that damage to the human *left* parietal lobe alone results in impairments in various number tasks [24]. So, what is the role of the right hemisphere? Semenza & Benavides-Varela [25] recruit a variety of methodologies to answer this question, from neurological patients and standard neuroimaging, to reversible inactivations induced by transcranial magnetic stimulation and direct current stimulation of the cortex. They conclude that there is a 'bilateral orchestration' of the left and right hemispheres, with the right, like the left, having small regions specific to each arithmetical operation, and perhaps being recruited when the problem to be solved is difficult.

Homologous regions supporting numerical tasks can be found in other primates [16]. Now similarities, or even equivalences, in behaviour across all these species are no guarantee that the mechanisms that produce them are the same. We cannot identify a kind of basic body shape or organ from which they all evolve, as we can for arms, legs and wings in chordates. It is, nonetheless, well established that the brain regions that underpin basic numerical processes in humans reside in the left and right parietal lobes, in particular, in the intraparietal sulcus.

It is interesting to note in this regard that neurons responding to numerosities have been in found in the *nidopallium caudolaterale* in the avian brain by Nieder [16]. The relationship, if any, of the *nidopallium caudolaterale* with the mammalian brain is, however, uncertain. The dominant view is that it would be equivalent, though not homologous, to the mammalian prefrontal cortex. This view is weakened by the fact that nidopallium differs from the mammalian prefrontal cortex in that it seems to lack connections with the hippocampal formation.

Whether different animals use similar (homologous or analogous) mechanisms for computing quantities is discussed in Vallortigara [19], with regard to both geometry and the mental number line. Overall, one can make a strong case for homology in encoding geometry in the hippocampal formation of vertebrates, from fish to mammals. For the mental number line, behavioural evidence is suggestive, but little is known on neural mechanism in these creatures, or even in the human brain.

By contrast, Rose [13] details a specific mechanism in neurons in the auditory midbrain in anurans for counting and calculating the number of sound pulses needed to attract female conspecifics and deter competing males.

4. Computational theories

Whereas there is broad consensus that animals from many phyla perceive numerosity and reason about it arithmetically, there is no consensus about what an appropriate computational theory of this ability should look like. Three papers elaborate three very different theories. Gallistel [26] suggests that the symbols for number are realized at the molecular level and form the basis for the brain's ability to represent every kind of quantity, not just numerosity. His theory attributes Weber's Law to the limited number of bits used to represent magnitudes across the many orders of magnitudes. He calls attention to the fact that fixed-point schemes for representing number obey Weber's Law. Hannagan *et al.* [27] suggest that numbers are coded by vectors of activation across multiple cortical units. Successive integers are obtained through multiplication by a fixed but random matrix. Their scheme also generates Weber's Law. Zorzi & Testolin [28] develop a scheme in which the neural representation emerges from the interaction between deep neural networks endowed with basic visual processing when confronted with visually experienced sets. Their scheme also exhibits Weber's Law-like properties.

5. Modality specificity and modality independence

Numerical abilities in the non-human species described in this issue are largely confined to a single modality: in monkeys, birds and bees vision, and in anurans, audition. Its numerosity is, however, an abstract, amodal property of a set, as Giaquinto [3] explains. Although Benson-Amram *et al.* [15] rely on auditory playback experiments of mammals in the wild, it seems likely that when lions and hyenas make numerical assessments of their own group and a competing group, they will use not only auditory information about the unseen competitors but also visual and other modalities to assess the number of their own group, and hence make a cross-modal comparison of numerosities. In fact, laboratory experiments show that monkeys and human infants can make cross-modal numerical comparisons between vision and audition (e.g. [29,30]). It not yet clear whether this is true in other species.

Burr *et al.* [31] have proposed that, in humans, numerosity is a primary visual property of a scene in the same way that colour, contrast, size and speed are, and that the brain deploys three visual mechanisms for making numerical discrimination depending on the number of visual elements: for numerosities approximately less than or equal to 4 (subitizing), 4–9 (serial enumeration) and large numbers where the elements are too crowded to parse. In this last case, a quite different mechanism takes over. However, they also note that representations of visual numerosities can be influenced by auditory numerosities, and vice versa, suggesting that humans do indeed represent number amodally.

6. Genetics

The fact that newborn chicks, fish and human neonates can make numerical discriminations suggests that this capacity does not arise as a result of interaction with the environment, but is inherited though subsequent interaction with environment doubtless modifies and refines the operation of this mechanism. It is also the case, as Butterworth [2] points out, that individual differences in numerical abilities have a substantial genetic component, perhaps as much as 30% of the variance in systematic twin studies. This suggests that the *starter kit* for learning arithmetic in school includes a domain-specific mechanism for representing numerosities, and that individual differences in this mechanism may explain why about 5% children (and adults), despite good formal education, have such trouble in learning arithmetic (though not necessarily other branches of mathematics, such as geometry). There is now an extensive literature linking poor numerosity discrimination or identification with poor arithmetical competence, even when other cognitive factors are taken into account. Burr *et al.* [31] suggest that of their three mechanisms, it is the enumeration mechanism that is most closely linked to arithmetical competence.

7. Implications

We now understand that the capacity to represent abstract magnitudes such as distance, duration and the numerosity of a set are foundational brain functions, with ancient evolutionary roots. This understanding spurs increasingly widespread research on the neurobiology and the genetics of these foundational mechanisms. In particular, it now seems clear that what may be learned from studies of animals far removed from humans on the evolutionary bush (zebra fish, for example) may reveal mechanisms for representing abstract quantities in their brains that are also found in human brains. Insofar as these mechanisms are foundations of human cognition and insofar as their abnormal function has far-reaching cognitive consequences, it is not inconceivable that in the far-distant future, gene-editing technology might be applied to the remediation of inherited defects in a human's most abstract thoughts, thoughts about number.

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