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Biological foundations of numerical thinking

Response to T.J. Simon (1999)

Elizabeth Spelke and Stanislas Dehaene

We are indebted to Tony Simon for raising discussion of the foundations of number processing [Simon, T.J. (1999) The foundations of numerical thinking in a brain without numbers *Trends Cognit. Sci.* 3, 363–364][1]. Simon's remarks bear on two theoretical issues. First, what is the specificity of the cerebral circuits for number processing? Second, how do numerical abilities emerge in the course of development? Simon's answers are clear-cut: the brain's cerebral circuits are 'non-numerical', and the developmental foundations of numerical processing are to be found in 'a brain without numbers' which constructs itself through unspecified mechanisms of 'open-ended plasticity'. We disagree on all counts. Although those important issues are still open to scientific inquiry, there is already strong evidence that the numerical abilities of the human brain rest in part on specialized cerebral processes and follow a specific developmental time course that hints at an initial specialization.

Specialized cerebral circuits for number processing

Our behavioral and brain-imaging results indicate that the rote learning of arithmetic tables is based on a linguistic representation of numbers, and therefore that such learning requires the 'recycling' of initially non-numerical brain circuits, such as language circuits, for the purpose of mathematics[2]. However, is that the case for *all* of our mathematical competences? Our research has uncovered a second cerebral circuit that depends on the left and right intraparietal regions, underlies the understanding of proximity relations between numerical quantities, and is particularly important for approximation and number comparison. We view this circuit as providing a biological foundation for number sense.

Three types of findings support the notion that the inferior parietal cortices contribute to a biologically determined numerical representation. First, left inferior parietal lesions can specifically impair the understanding and processing of numbers[3,4]. Conversely, the category of number can also be selectively preserved in the presence of severe deficits in the processing of other categories of words[5]. The dissociation between preserved and impaired knowledge can be remarkably sharp. For example, patient 'MAR' was at chance in deciding which number falls between two others (he responded that the number that falls between 1 and 3 was 7), yet he had no trouble performing similar bisection tasks with letters, months, days of the week or notes of the musical scale. Such category-specific deficits exist for other domains as well. For instance, a remarkably restricted impairment of the knowledge of animals was recently described[6]. Based on such cases, the suggestion has been made that, through brain evolution, specialized regions of the brain have emerged for the representation and manipulation of evolutionarily relevant environmental categories, such as animals, persons, or foods[2,6]. Number also appears to be such a category.

A second finding comes from cross-cultural comparisons of the cerebral bases of calculation, which provide evidence that the association of arithmetical function with the intraparietal sulcus is remarkably reproducible. If arithmetic were just a cultural activity without a strong foundation in brain architecture, one would expect considerable variation, depending on learning, education and culture. Yet reports from research groups in various countries suggest that, in most if not all cultures throughout the world, the sites of the lesions causing a loss of number sense, as well as the sites of brain activation during calculation, systematically fall in the inferior parietal region (see Ref. 7 for a review).

The third source of evidence that speaks against Simon's notion of 'open-ended plasticity' comes from studies of developmental dyscalculia, which indicate that the contribution of the inferior parietal cortices to number processing is highly specific and cannot be easily transferred to other brain regions. Some children show a selective category-specific deficit for number processing[8,9]. In spite of their normal intelligence, normal language acquisition, and the special education that they received, they were never able to acquire the concept of number. They have to rely on laborious verbal-counting strategies even for tasks as simple as determining that nine is larger than three, or that a duck has two legs. Although few accurate brain-imaging data are available on patients with developmental dyscalculia, in at least one case the deficit has been related to early brain damage restricted to a small region of left inferior parietal cortex[10]. Thus, the parietal circuit would appear to be functional during development to such an extent that its lesioning causes a complete failure of arithmetic development. Such evidence is hard to reconcile with the idea, implicit in Simon's comment, that the brain is a general learning device. There is, of course, no denying that learning occurs in the mathematical domain. But learning might be based on specialized domain-specific systems rather than on a general constructivist scheme.

Note that the postulated role of parietal circuitry in providing a biologically determined sense of number does not imply that arithmetic is the *only* function of that circuit. It is naive to expect current brain-imaging techniques to reveal a single portion of brain tissue that is responsive only to numbers. Rather, the extent of our observed activations hints at the possibility of a considerable overlap with other visuospatial functions that are known to yield very similar activity patterns in the intraparietal sulcus, such as mental rotation and other spatial-coordinate-transformation tasks. Simulations in neural networks suggest that a representation of numerical quantity can emerge naturally from the extraction of object-location information, independently of object identity[11]. Because these functions are performed within the dorsal occipito-parietal pathway, parietal circuitry might have needed only minimal alteration in the course of evolution to become biased to encode numerosity information. Numerical and spatial representations might thus be intricately intertwined in the parietal lobe. It is possible that they can only be distinguished empirically by their internal micro-circuitry or their pattern of connectivity to other brain areas.

Phylogeny and ontogeny of numerical representations

Because our article was concerned only with the performance of human adults, it does not in itself address the questions at the heart of Simon's essay, which concern the phylogeny and ontogeny of numerical representations. There is,

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however, a wealth of animal and developmental research that is pertinent to these topics, and much of that research also fails to support Simon's thesis of 'a brain without numbers'.

Let us begin with phylogeny. If evolution did not produce a brain with the capacity to represent number, and if that capacity emerged in humans only through culturally transmitted activities unique to us, such as finger counting, then other animals should show no capacity to represent numerosity. Contrary to this prediction, a wealth of research by behavioral ecologists and comparative psychologists provides evidence for capacities to represent numerosity in animals including birds, rodents, and primates (for reviews, see Refs 2,12). Abilities to discriminate between sets of different numbers of items, and to base that discrimination on number rather than on other perceptual variables such as spatial extent or temporal duration, have been found in numerous experiments. For example, laboratory rats, parrots and monkeys have been trained to respond to a specific number of objects or events[13–15], and untrained monkeys and apes have been found to choose spontaneously the more numerous of two sets of food items[16,17]. Because no non-human animal (with the possible exception of language-trained chimpanzees) has been observed to engage in finger-counting, these findings fail to support the claim that the sense of number results from such activities. More positively, the findings provide evidence that a capacity to represent number evolved before humans did and is shared by many vertebrates.

Turning to ontogeny, we can ask whether Simon's account nevertheless is true of humans: do human infants represent and track up to four objects, but otherwise fail to represent sets and larger numbers? It is possible that representations of objects, rather than explicit representations of numerosity, underlie infants' performance in Wynn's addition and subtraction tasks[18] and in number-discrimination tasks that present small numbers of objects[19]. Such representations cannot, however, account for infants' performance in a variety of other situations. Experiments provide evidence that young infants can enumerate entities that are not material objects, including speech sounds[20] and actions such as jumping[21]. Moreover, infants can distinguish between sets whose numerosities exceed the limits on object representations: preliminary evidence suggests that they can distinguish displays of 8 versus 16 dots when variables such as spatial extent, density and brightness are controlled (F. Xu and E. Spelke, unpublished data). All these findings provide evidence for representations of number that exceed the scope and power of mechanisms of object tracking (see Ref. 22 for a review).

Despite the evidence for phylogenetic and ontogenetic continuity in number representations, human number representations do have unique features. In particular, only humans who have learned symbolic counting appear to represent the exact numerosities of sets with no upper limit. When animals are trained to make exact-number discriminations, training becomes increasingly difficult, and performance increasingly error prone, with increasing numerosity[15,23]. In the absence of such training, discriminability is proportional to set size, in accordance with the Weber–Fechner law[12]. Human infants also discriminate between large numerosities only when the difference ratio also is large: infants have been found successfully to distinguish 8 from 16 dots but not 8 from 12 dots (F. Xu and E. Spelke, unpublished data). Once children learn verbal counting, however, they come spontaneously to use counting to represent large numerosities exactly[24,25]. It is possible that the involvement of language areas of the brain in the memorization of exact arithmetic facts is rooted in this acquisition.

In summary, we share with Simon the hypothesis that some mathematical abilities, particularly those that are evidently late cultural acquisitions, such as multiplication tables, do not rely on specific cerebral substrates. The unique and culture-specific features of human number knowledge nevertheless appear to build on a dedicated neural and cognitive system: a number sense that emerged early in vertebrate evolution, is present and functional early in human development, and resides in dedicated neural circuitry.

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