Update

Research Focus

# The ABC of cardinal and ordinal number representations

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**Numerical cognition encompasses the concepts of quantity ('how many?') and serial order ('which position?'). Yet, although numbers can convey different meanings, a recent imaging study by Fias and coworkers showed that ranking letters in the alphabet is subserved by a cortical network highly similar to that involved in judging magnitudes. In terms of neural processing, quantity and rank might just be two sides of the same coin.**

## The conceptual segregation

When thinking about numbers, the first aspect that usually comes to mind is that they denote numerical quantities, or cardinality (e.g. 'eight buses'). However, numbers can do more [1]. We also use them to signify the position of an item in an ordered sequence – that is, its rank – thereby exploiting their ordinal meaning ('eighth bus'). Finally, by drawing on their nominal aspect, we can also use numbers to indicate the identity of something ('bus number eight'). Yet, despite this partitioning of numerical competence on conceptual grounds, a recent study by Fias *et al*. [2] suggests that mental processing of cardinal and ordinal numbers is based on neural networks housed within the same cortical structures.

## Common processing of cardinal and ordinal numbers

So far, the cardinal and ordinal aspects of numbers have almost exclusively been considered in isolation, ignoring the possibility that quantity and rank might actually be based on the same neural system; after all, both are integral parts of numerical competence. At last, Fias *et al*. [2] have now made an attempt at closing this gap. Using functional magnetic resonance imaging (fMRI), the authors studied healthy subjects while performing tasks that required access to numerical information. Participants were asked to compare and indicate by button presses which of two letters came later in the alphabet, and the blood oxygenation level-dependent (BOLD) activations – taken as a correlate for neuronal activity – were compared with those obtained while they determined which of two numbers was larger. A control task was designed, in which subjects had to decide which of two color stimuli was more saturated, to ensure that the resulting BOLD activity was specific for numerical comparisons rather than due to comparative judgments *per se*. In addition, to rule out other unspecific cognitive factors, such as intentional response selection, attention shifting and motor preparation, each comparison task was further controlled by a dimming detection task using identical sensory input and motor responses. The results clearly showed that comparisons of letters and numbers are subserved by a highly similar neural network spanning the bilateral parietal, occipital and temporal cortices, in addition to frontal areas (Figure 1a). Although the number comparison was interpreted by the authors as addressing the quantitative aspect of numerical cognition (and designed to contrast the letter task), it could also be based on the ranking of elements in the number sequence alone (ordinal aspect). This notion aside, it was intriguing to find that the strongest activation for the number and letter tasks clustered around the intraparietal sulci (IPS), coinciding precisely with the areas reported previously for numerical quantity processing [3]. In terms of neural processing, quantity and rank might just be two sides of the same coin.

## Ordered sequences: the number line and the alphabet

Letters might be ideal stimuli to investigate pure ordinal effects because the alphabet is a strictly and overlearned ordered succession of items devoid of any cardinal information. Every child knows (through nursery rhymes, for instance) that 'a' is first, 'b' second, 'c' third and so on. Interestingly, both the alphabet and numbers seem to be represented on a 'mental line' that is oriented from left to right in our Western culture [the so-called Spatial Numerical Association of Response Codes (SNARC) effect] [4]. More precisely, we respond faster with the left hand both to small numbers (beginning of the number line) and to letters at the beginning of the alphabet (a,b,c...) than to large numbers and letters at the end of the alphabet [5]. In addition, the discrimination of both number sequences and letters of the alphabet is characterized by the distance effect; that is, the ability to discriminate between two numbers or letters improves (with regard to reaction time and precision) as the (numerical or alphabetical) distance between the items increases [6,7]. This might indicate that the positions of items in sequences are encoded approximately by tuning functions; numbers and letter positions are determined from a continuum of partially overlapping, nondiscrete representations. Thus, on a behavioral level, cardinal and ordinal numbers have much in common.

## Loss of numbers and sequences

A second line of evidence arguing for shared cortical structures underlying quantity and sequence order processing comes from a neuropsychological study of a patient

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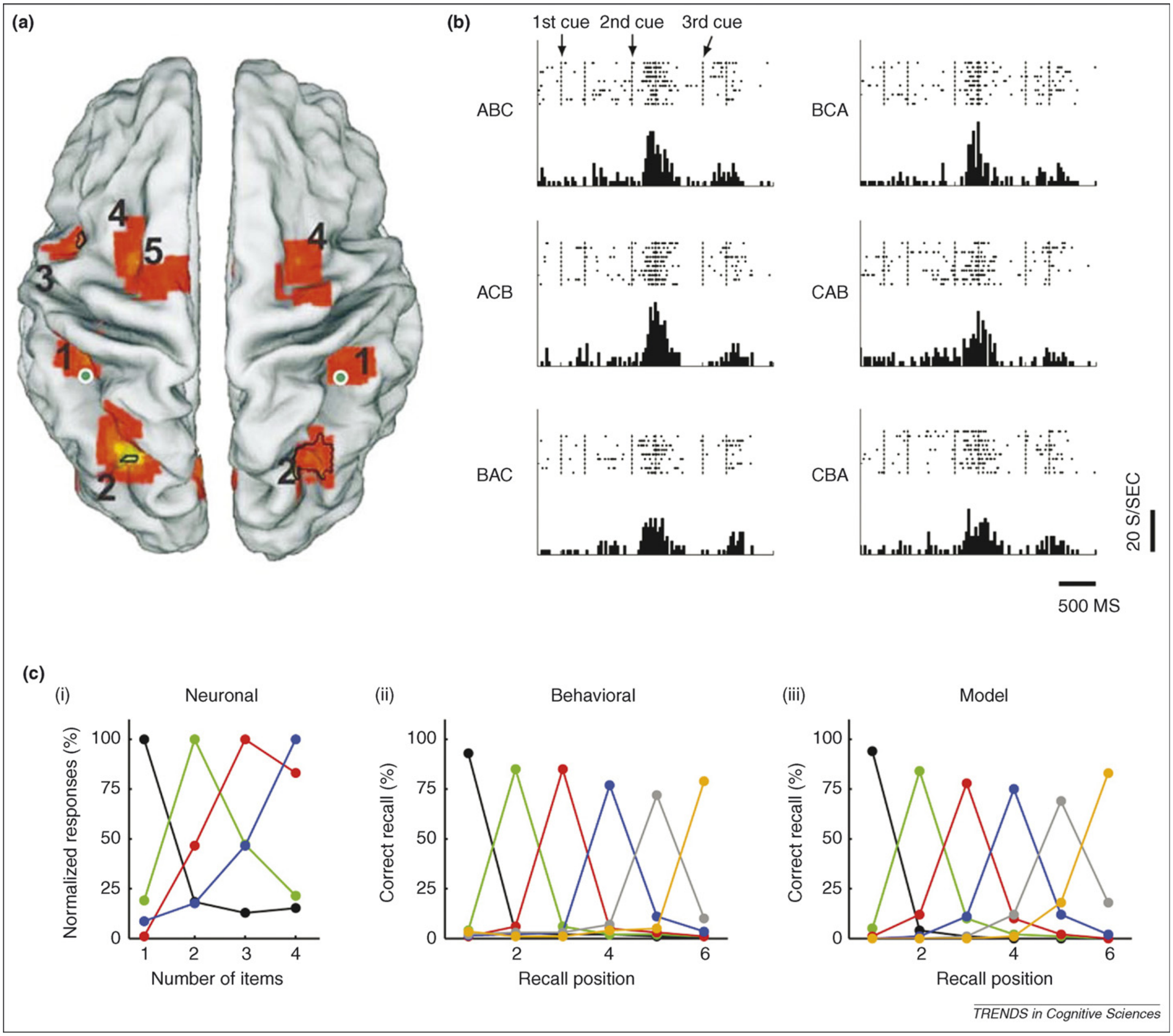


**Figure 1**. Neural processing of ordinality in primate frontoparietal cortex. **(a)** Top view of a human brain (up is anterior) showing cortical regions subserving both number and letter comparisons (color coded) during fMRI scanning. Whereas the posterior parietal cortex (2) is also activated by comparison of object saturation (black contours indicate the conjunction of numbers, letters and saturation), the anterior IPS (1) and frontal regions [ventral precentral (3), dorsal precentral (4) and superior frontal cortex, (5)] process numbers and letters only. Green dots show the main focus of numerical processing in the IPS, as determined by a meta-analysis [3]. Reproduced, with permission, from Ref. [2]. **(b)** Responses from a PFC neuron in monkeys trained to observe and remember the order in which three visual objects appeared. The neuron encoded the second rank, irrespective of the order in which the three cues (symbolized by letters ABC) were presented. Neural responses are shown in a dot-raster histogram (top panel of each histogram; each dot represents an action potential) and averaged as peri-stimulus time histograms (bottom panels). Modified, with permission, from Ref. [13]. **(c)** Coding of sequential position information. (i) Average tuning curves of IPS neurons recorded in monkeys trained to add up sequentially presented single dots. The discharge rate of the cells was maximal at a preferred numerosity (color coded) and gradually dropped off with increasing numerical distance. Data derived from Ref. [11]. (ii) In behavioral experiments, the percentage of correct serial recall depends on the position of the item within a sequence. The first and last items are recalled with increased accuracy (primacy and recency effect, respectively) [15]. (iii) Computational model of serial order in working memory. The simulation uses information from neuronal item and rank representation to reproduce the behavioral data. The individual plots peak at the correct recall position, and there are fewer errors confusing two positions as the distance between these positions increases. Modified, with permission, from Ref. [12].

suffering a left frontoparietal stroke. Cipolotti *et al.* [8] reported one patient with a severe and selective deficit in processing numbers (with the exception of small numbers, below about four). Interestingly, this patient also showed poor performance on reciting non-numerical sequences such as letters, days of the week and months of the year. However, such single-case studies of patients with often large and variable lesions need to be interpreted with caution, and it should be noted that other neuropsychological findings support the contrary view, namely that there are distinct brain structures responsible for quantity and sequence order processing [9].

## The code for quantity and order

Indirect evidence that quantity and rank processing might recruit a common neural substrate had previously been collected by extrapolating from studies of the individual tasks. Numerical quantity activates specific frontal and parietal regions, with the cortical structures surrounding the IPS having a central role. A similar frontoparietal network was found to be recruited when the order of two letters in a previously memorized sequence had to be judged [10]. Thus, given their neural and behavioral similarities, sequences and numerical quantity might be represented by similar tuning functions.

The neuronal code for nonverbal quantity has been analyzed in non-human primates trained to perform precise cardinal judgments on sets of dots [11]. Neurons both around the IPS and in the prefrontal cortex (PFC) showed peak discharge to preferred numerosities and a systematic drop-off in activity as the numerosity varied from the favored one. Neurons with adjacent preferred numerosities have overlapping tuning functions, coding discrete quantities as if they were placed along a continuum of magnitude. Such a nonverbal magnitude code has been demonstrated both for numerosities of multiple-dot displays and for single dots presented sequentially one by one [11] [Figure 1c (i)].

### Modeling order representation

The sequential presentation of single items bears not only a cardinal component (which the monkeys were trained to judge [11]), but also an ordinal aspect, given that the first item is followed by the second, third and so on. Botvinick and Watanabe [12] recently elaborated a computational model of working memory for serial order by weaving together item, numerosity and rank information. Their network combined graded neuronal responses to different items (not yet verified experimentally) and tuning functions for sequential enumeration processes [11], with data showing that neurons in the PFC code the rank of items within a sequence [13] (Figure 1b). The output of the model, a recalled multi-item sequence, replicated many behavioral characteristics of working memory, such as the primacy effect (a recall advantage for initial items) and the recency effect (advantage for the last one or two items) [Figure 1c, (ii,iii)]. Furthermore, changing the width of the tuning curve for rank in this model simulated the developmental finding of improved recall accuracy with age. Thus, this model integrates across several neurophysiological studies to demonstrate how higher cognitive functions might exploit both quantity and rank. It posits that working memory of ordered sequences relies, at least in part, on neuronal assemblies in the parietal cortex and PFC that also contribute to numerosity representations.

### Neurons coding both quantity and rank?

The study by Fias *et al.* [2] showed convincingly that the cortical network for rank coincides with the previously reported areas processing numerical quantity. Given the limited spatial and temporal resolution of fMRI, however, this does not necessarily mean that single neurons might encode both cardinality and ordinality. So far, single-cell studies in monkeys have concentrated on either cardinal or ordinal aspects but never both. Based on the findings that discrete and continuous quantities [14], and even simultaneously and sequentially presented numerosities [11], are encoded by largely distinct neuronal populations in the IPS, we would predict that cellular segregation also occurs for the processing of cardinal and ordinal stimulus aspects. Single-cell electrophysiology is well poised to answer this important question in the years to come, determining whether quantity and rank might share the concept of number but not the cellular substrate.

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doi:10.1016/j.tics.2007.11.006