

Topographic representation of high-level cognition: numerosity or sensory processing?

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A recent study showed that topographic field maps of complex cognitive functions, such as numerosity, exist in the human brain. This is an exciting, novel approach for studying the neural representation of high-level cognition. However, the results can also be explained on the basis of the confounding non-numerical sensory cues of numerosity.

Topographic representations in sensory cortices reflect the layout of the respective organs. For instance, in the occipital cortex, the receptive fields of adjacent neurons represent slightly overlapping but adjacent areas of the visual field [1]. Topographic field maps are primarily studied in primary sensory cortices but they are also present in higher cortical association areas. For instance, the parietal lobe, which is involved in complex cognitive processes, such as sensory integration, working memory, and numerical cognition, also supports topographic field maps [1]. In a recent study, Harvey and colleagues [2] investigated whether topographic representations for primary sensory processes also underlie more complex cognitive processes, including numerosity.

Numerosity is an ideal model for studying the topographical representation of cognition because it is a semantic concept with clear spatial distribution. This spatial organization is described by the ‘mental number line’ metaphor, which states that numerosities are represented as a line that runs from left to right with increasing magnitude [3]. Furthermore, imaging and neurophysiological studies have shown that the underlying neural architecture of number representations closely resembles that of low-level sensory processes [4,5]. The neuronal populations implicated in numerical representation are tuned to a preferred number, a phenomenon termed number selective coding [4]. These tuning curves follow a Gaussian distribution, the width of which reflects the amount of overlap in preferred number between neighboring neuronal populations (Figure 1A).

To investigate the existence of topographic numerical representation, Harvey *et al.* presented participants with digits (Arabic numerals) and numerosities (arrays of dots) between 1 and 7 while measuring neural activity using high-field 7 Tesla functional MRI. A neural model that describes Gaussian functions, similar to models used to study visual field maps, was employed to pinpoint the areas showing numerosity-selective tuning. The right posterior parietal lobe showed a topographic representation, reflecting a pref-

erence for numerosity information that shifted from medial to lateral areas as numerosity increased (Figure 1B). The cortical surface area devoted to a preferred numerosity decreased with increasing numerosity and the tuning curves became wider for larger numerosities. Both findings suggest more precise numerosity selectivity for small than for large numerosities. However, Harvey *et al.* did not find a topographic map for digits and concluded that this might be located in a different brain region.

This study demonstrates that cortical organization of complex cognitive functions can be studied using topographic field maps. It also presents results that bear on theoretical issues pertaining to numerical cognition, including the role played by sensory cues in numerosity processing and the nature of numerical representations.

It is highly debated whether numerosity processes can be explained by their confounding sensory cues [6,7]. To address this problem, Harvey *et al.* included five sensory control conditions. In each condition, a single sensory cue was kept constant (e.g., diameter, circumference). It was observed that preferred numerosity tuning was significantly different in circumference compared to the other sensory control conditions (Figure 1C). Harvey *et al.* noted that the constant circumference condition had very different dot sizes (Figure 1D) and concluded that neurons in a single cortical region could encode numerosity or a sensory cue, or both at the same time (see also [8]). Thus, numerosity neurons exist, but the more abundant sensory neurons within the same voxel obscured pure numerosity tuning in the circumference condition.

This explanation, however, implies that in the remaining sensory control conditions, where the majority of sensory cues and numerosity were confounded, the sensory neurons also dominated the signal. Hence, a fully sensory-based explanation that does not require the existence of numerosity-selective neurons is also plausible. Numerosity is typically defined by its sensory cues: when numerosity increases, its sensory cues also increase. This positive relationship between numerosity and its sensory cues was present in the numerosity stimuli except in the circumference control condition, where most sensory cues decreased while numerosity increased. The topographic map of preferred numerosity tuning observed by Harvey *et al.* therefore likely reflects a weighted response of neurons that encode different sensory cues rather than a pure numerosity estimate. This proposal is in line with previous studies [6,7] and challenges current models of numerical cognition [9] that assume that a

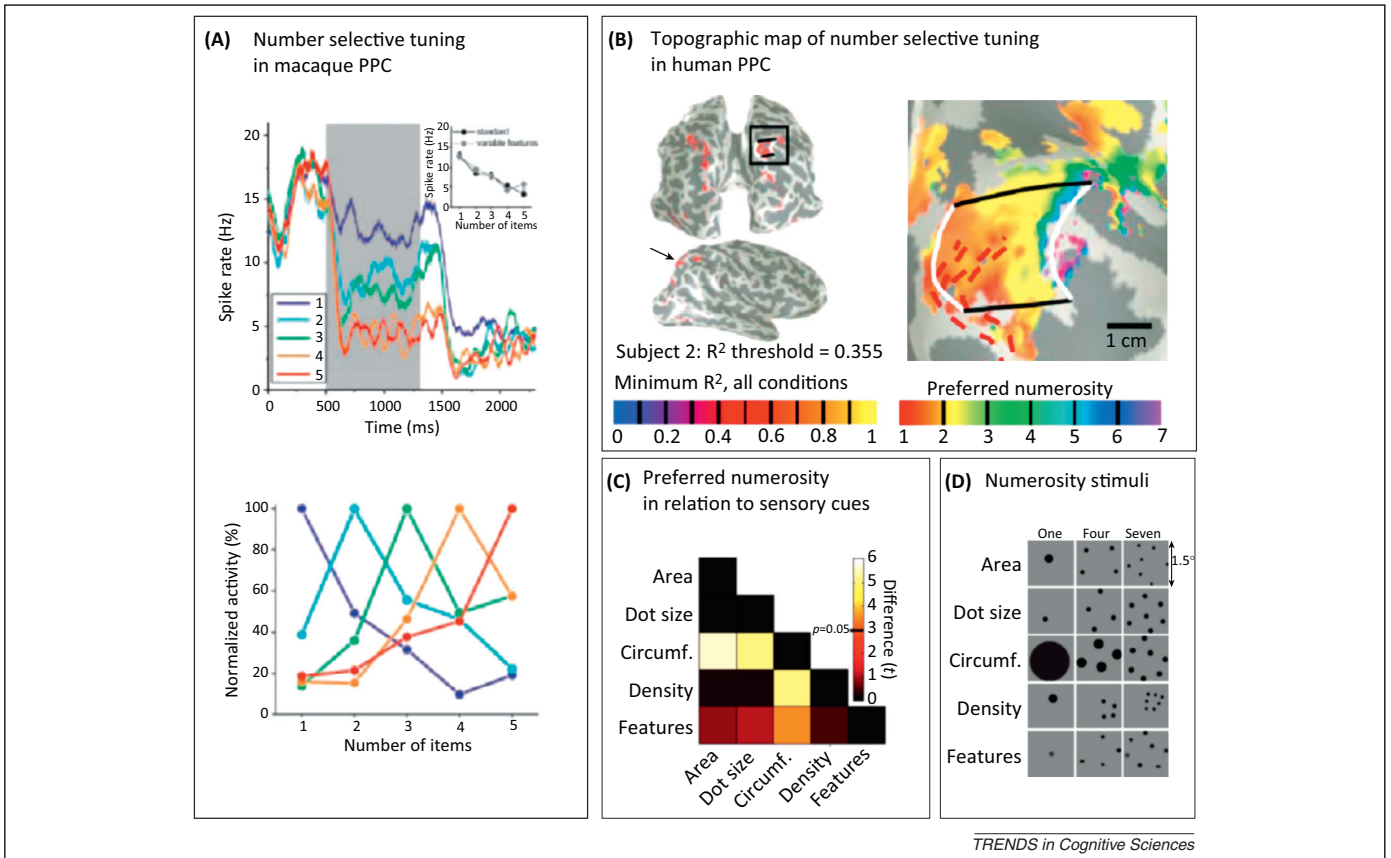


Figure 1. Number selective tuning in the macaque and human posterior parietal cortex. **(A)** An example of a neuron that is selectively tuned to a numerosity of one (upper panel) and neuronal activity that decreases with increasing numerical distance (lower panel). Adapted, with permission, from [4]. **(B)** Topographic representation of numerosity is present in the human posterior parietal cortex. Preference for numerosity information shifts from medial to lateral brain areas with increasing numerosity. Adapted, with permission, from [2]. **(C)** Comparison of numerosity preferences across recording points in different stimulus conditions, averaged across subjects. The numerosity preference differed between visual control conditions, particularly in the constant circumference condition. This finding indicates that preferred numerosity tuning was not invariant to changes in circumference. Adapted, with permission, from [2]. **(D)** Most sensory cues increased with increasing numerosity, except for the stimuli in the circumference control condition. Adapted, with permission, from [2].

single neuronal population responds to its preferred numerosity regardless of the type of sensory control applied and that this tuning is independent of the type of number stimulus (dots or digits).

A sensory-based explanation is consistent with the fact that visual field maps for sensory processes of different complexity exist in the parietal cortex and that at the same time the parietal cortex supports the integration of different sensory stimuli [1]. It also better explains the absence of number selective tuning for digits because, in contrast to numerosity, digits and their sensory properties are not confounded. The finding that numerosities are dissociated from digits also provides support for multiple, non-abstract representations of numbers [10].

In sum, can we conclude that a topographic cortical organization exists for high-level cognitive domains, such as numbers? The current findings suggest a spatial distribution for numerosity processes akin to topographic maps in sensory perception. However, preferred tuning to digits was not present in this area. This, together with the fact that preferred numerosity tuning was not invariant to sensory cues, questions whether semantic concepts are represented in a topographic manner.

Harvey *et al.*'s work and our competing explanation open up many exciting opportunities for future research, such as the range of numerosities that are represented at the neural

level, the link between topographic representation and individual differences in cognition, including learning disabilities such as dyscalculia (e.g., would people with poorer numerical abilities have less refined topographic representations?), and the impact of education and rehabilitation on such topographic representations. However, before pursuing these directions, a more precise definition of numerosity is required. The current findings suggest that, in contrast to digits, numerosity is not a semantic concept that is extracted from sensory input. Sensory cues influence or maybe even explain preferred numerosity tuning. Numerosity could therefore be defined as a weighing of different sensory cues to obtain a numerosity estimate.

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References

- 1 Silver, M.A. and Kastner, S. (2009) Topographic maps in human frontal and parietal cortex. *Trends Cogn. Sci.* 13, 488–495
- 2 Harvey, B.M. *et al.* (2013) Topographic representation of numerosity in the human parietal cortex. *Science* 341, 1123–1126
- 3 van Dijck, J-P. *et al.* (2013) Linking numbers to space: from the mental number line towards a hybrid account. In *The Handbook of Numerical Cognition* (Cohen Kadosh, R. and Dowker, A., eds), Oxford University Press (in press)

- 4 Nieder, A. and Miller, E.K. (2004) A parieto-frontal network for visual numerical information in the monkey. *Proc. Natl. Acad. Sci. U.S.A.* 101, 7457–7462
- 5 Piazza, M. *et al.* (2004) Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44, 547–555
- 6 Gebuis, T. and Reynvoet, B. (2012) The interplay between nonsymbolic number and its continuous visual properties. *J. Exp. Psychol. Gen.* 141, 642–648
- 7 Dakin, S.C. *et al.* (2012) A common visual metric for approximate number and density. *Proc. Natl. Acad. Sci. U.S.A.* 108, 19552–19557
- 8 Tudusciuc, O. and Nieder, A. (2007) Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proc. Natl. Acad. Sci. U.S.A.* 104, 14513–14518
- 9 Stoianov, I. and Zorzi, M. (2012) Emergence of a ‘visual number sense’ in hierarchical generative models. *Nat. Neurosci.* 15, 194–196
- 10 Cohen Kadosh, R. and Walsh, V. (2009) Numerical representation in the parietal lobes: abstract or not abstract? *Behav. Brain Sci.* 32, 313–328

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Fear not: manipulating sleep might help you forget

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Memory storage is not static – updating is often needed. When it comes to traumatic memories, forgetting may be desired. Two innovative studies recently demonstrated that fear memories can be weakened during sleep using odors associated with fear-learning episodes. New strategies along these lines should be carefully considered for treating unwanted fears.

In the film *Eternal Sunshine of the Spotless Mind* (2004), two ex-lovers attempt to get over a painful breakup through an incredible treatment that erases their memories of each other. Today, this is science-fiction – and very far from scientific fact. However, two recent studies take a step in this direction by successfully attenuating fear memories during sleep. These findings may lead to new hope for people suffering from maladaptive memories, perhaps even traumatic memories at the root of phobia or post-traumatic stress disorder (PTSD).

During sleep, patterns of brain activity elicited during learning are spontaneously reactivated, a process thought to make memories stronger and more enduring [1]. Furthermore, it is possible to externally influence which memories are reactivated during sleep by using sensory cues (e.g., odorants or sounds) as reminders of the previous learning [2]. So far, this ‘targeted memory reactivation’ (TMR) has been shown to strengthen visuospatial memory, skill learning, and word recall [3–6]. But can TMR suppress or at least weaken painful features of a bad memory?

In a new study conducted by Rolls and colleagues, mice were conditioned to fear amyl acetate, which smells like banana [7]. This odor stimulus was systematically followed by painful foot-shock during conditioning. After a 24-h interval, which ensured sufficient consolidation of the fear memory, the odorant was reapplied during sleep. Parallelizing previous studies using TMR, externally reactivating the fear memory in conditioned mice facilitated fear behavior the following day, as indicated by increased freezing when the conditioned stimulus (CS odor) was delivered alone in a new context. However, the goal was to suppress

fear memories, not reinforce them. To reverse the effect of the sleep manipulation, the researchers injected a protein-synthesis inhibitor in the amygdala before applying the CS odor during sleep. This manipulation has been successfully used to attenuate fear memory in the awake state [8], based on the idea that enduring memory storage requires protein synthesis during a critical time period after learning. Consistent with expectations, injection of the protein-synthesis inhibitor, combined with subsequent external reactivation of the fear memory during sleep, led to a diminution of fear expression the following day. Appropriate controls confirmed that the fear-memory attenuation was not due to the protein-synthesis inhibitor itself nor to nonspecific effects of odorant presentation.

Hauner and colleagues used different procedures to suppress fear memory in humans [9]. In this study, 15 young subjects underwent contextual fear conditioning, in which face images were associated with an uncomfortable electrical shock while an odor was in the background (e.g., mint, lemon, pine). After conditioning, the faces elicited a fear response demonstrated by increased skin conductance.

Surprisingly, and contrary to Rolls *et al.*’s results, reapplying the odorant during an afternoon nap did not reinforce fear memories. Instead, the odor manipulation reduced fear responses for the corresponding faces relative to other faces for which the corresponding odor context had not been reactivated during sleep. These other faces had the same conditioned association with shock and with a different odor, matched for pleasantness, assuring that TMR effects were specific to the cued association. This targeted fear extinction during sleep was accompanied by a decrease in hippocampal functional MRI activity and a reorganization of ensemble pattern activity in the amygdala from pre- to post-sleep. Whether this fear reduction reflected true erasure of the fear memory, reduction of the emotional salience of the memory, or a new memory trace associated with safety remains unclear.

How can the apparent discrepancy between the two studies – that TMR in the mouse study strengthened fear memory whereas TMR in the human study reduced it – be explained? Aside from species differences, there were also