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Forum

Semantic cognition versus numerical cognition: a topographical perspective

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Semantic cognition and numerical cognition are dissociable faculties with separable neural mechanisms. However, recent advances in the cortical topography of the temporal and parietal lobes have revealed a common organisational principle for the neural representations of semantics and numbers. We discuss their convergence and divergence through the prism of topography.

Semantic processing versus numerical processing

Traditionally, in neuropsychology and neuroimaging, **semantic cognition** (see Glossary) and **numerical cognition** are pitted against each other, each serving as a control condition for the other domain. For example, research on neurological disorders has demonstrated a double dissociation: individuals with **semantic dementia** preserve mathematical ability despite profound impairments in semantic tasks, whereas individuals with **dyscalculia** retain semantic proficiency despite struggles with processing numbers. A similar comparison is seen in the design of cognitive neuroimaging studies: to reveal semantic regions in the temporal cortex, number tasks have been used as control conditions for contrast [1], whereas to identify numerical regions in the parietal cortex, semantic tasks have been used for contrast [2].

While semantic and numerical abilities are viewed as two dissociable faculties underpinned by separable neural mechanisms, recent progress in connectome research has revealed that they share a similar neurocomputational principle that guides the processes of distilling abstract meaning from sensory–motor experiences and drives the formation of unique patterns of **cortical topography**. With advances in cortical cartography of the human brain, we have begun to understand how semantic and numerical knowledge emerge from the integration of distinct sensory–motor information in different zones. The cortical regions specialised for representing semantic meaning and numerical quantity are situated between different primary sensory–motor systems and thus receive distinct combinations of inputs. As a consequence of this cortical juxtaposition, the same mechanisms of multimodal integration can engender qualitatively distinct representations (semantic vs. numerical). Herein we first highlight the striking parallel in their cortical arrangements: in both semantic and numerical domains, modality-specific representations encircle heteromodal representations. Then, we discuss how the integration and segregation of various streams of sensory–motor processing may sculpt neural representations.

The transmodal 'semantic' hub in the temporal cortex

The anterior temporal lobe (ATL) plays a critical role in representing semantic knowledge. Rather than being a homogeneous structure, functional tuning varies in a graded way across ATL subregions based on distinct connectivity to modality-specific cortices [3,4]. As shown in Figure 1, the inferomedial ATL preferentially tunes to visually based knowledge (concrete concepts) and pictorial stimuli; the superolateral ATL prefers verbally based knowledge (abstract concepts) and human speech, and the temporopolar cortex favours social knowledge over other semantic contents.

The functional preferences of different ATL subregions are reflected in their connectivity with various modality-related regions. Diffusion-based tractography and resting-state connectivity reveal that the inferomedial ATL receives direct input from the visual cortex, the superolateral ATL receives direct input from the auditory cortex, and the temporopolar cortex is directly connected with the orbitofrontal cortex (which is heavily involved in processing valence in social contexts). Critically, different threads of modality-

Glossary

Cortical gradient: the graded variation in functional or physiological features along the whole cortex. This can refer to connectivity, cortical microstructure, or gene expression. The principal gradient, which explains most variance, represents the progression from primary sensory/motoric cortices at one end to the high-order association cortices (e.g., the default-mode system) at the other end.
Cortical topography: the spatial arrangements of functional or physiological properties on the cortex. Such arrangements usually form a consistent macroscale spatial motif at the group level, although the precise topographical boundaries/extents may vary between individuals.
Dyscalculia: individuals with dyscalculia have difficulty efficiently processing numbers; this condition is found to be associated with functional and structural anomalies of the intraparietal sulcus.
Numerical cognition: the abilities to perceive quantity, extract numerosity, represent quantity in symbolic or nonsymbolic formats, and manipulate quantitative representations in a goal-directed fashion (e.g., arithmetic). Akin to semantic cognition, various numerical processes can also be categorised into two major dimensions: (i) representations of numerical meaning per se, and (ii) operations performed on numerical representations (e.g., subtraction, multiplication, division).
Semantic cognition: the abilities to (i) represent semantic meaning per se in both verbal format (e.g., lexical words) and nonverbal formats (e.g., visual/acoustic/motoric features), and (ii) operate on semantic representations in a goal-directed manner (e.g., composing a sentence by deliberately selecting particular words to express an intended meaning). These two abilities – representations and operations – are closely interacting yet dissociable at the cognitive and neural levels.
Semantic dementia: individuals with semantic dementia suffer from severe erosion of semantic memory owing to a lesion at the transmodal regions of the anterior temporal lobe.

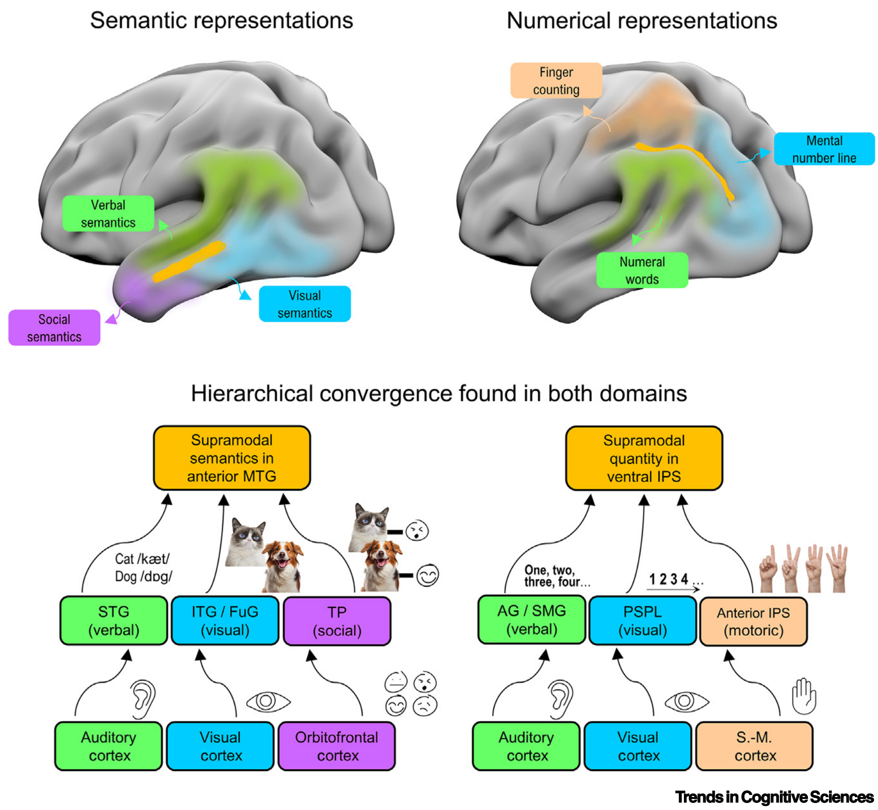

Figure 1. The topography and hierarchy of semantic/numeric processing. Despite their dissociable neural substrates, semantic meaning and numerical quantity emerge from similar cortical motifs, which reflects hierarchical integration from unimodal to supramodal. The supramodal regions are situated at central loci (illustrated by the yellow patches on the brain), topographically enclosed by modality-related regions in the periphery. This is further shaped by the surrounding cortical landscape (e.g., integration in the parietal 'how' pathway and the temporal 'what' pathway is geared towards distinct neurocomputational goals for action and identification, respectively). Abbreviations: AG, angular gyrus; FuG, fusiform gyrus; IPS, intraparietal sulcus; ITG, inferior temporal gyrus; MTG, middle temporal gyrus; PSPL, posterior superior parietal lobule; S.-M., sensorimotor; SMG, supramarginal gyrus; STG, superior temporal gyrus; TP, temporal pole.

related processing converge within the central subregion of the ventrolateral ATL, which functions as a transmodal hub of semantic representations. This hub is commonly engaged by semantic tasks, irrespective of various modalities and task requirements, and its lesion leads to transmodal semantic defects seen in semantic dementia patients. Within this structure, functional tuning and connectivity vary in a graded manner, with a heteromodal centroid and stronger modality biases in peripheral subregions.

The transmodal 'numerical' hub in the parietal cortex

The intraparietal sulcus (IPS) plays a fundamental role in representing numerical quantities. Decades of research have established that the IPS is invariably engaged by numerical processing no matter whether numbers are seen, heard, or gestured. Compared with the transmodality nature of the IPS, other subregions in the parietal lobe exhibit a modality bias. Verbal numerals and simple arithmetic facts are represented in the angular/supramarginal gyri (AG/SMG), the visuospatial representations of mental number line are represented in the posterior superior parietal lobule (PSPL), and the somatosensory representations of finger counting are encoded in the anterior IPS.

Based on connectivity methods, it has been demonstrated that these modality-biased regions preferentially connect with different sensory–motor systems [5]. The AG and SMG have a tight coupling with verbal language areas in the temporal lobe, the PSPL is closely linked with the occipital visual cortex, and the anterior IPS is intimately linked to the somatosensory/motor cortices. Crucially, different threads of unimodal processing, each emanating from different sensory systems, eventually converge at the ventral IPS in a graded fashion to form a supramodal quantity code that underlies the understanding of abstract numerosity. This graded transition, hierarchically transitioning from sensory–motoric into supramodal, echoes the sensorimotor perspective of numerical cognition [6] and, more importantly, reveals a topographical motif that resembles what happens in the temporal cortex for the representations of semantic knowledge (see Box 1 for a discussion about which aspect of semantic/numerical cognition particularly pertains to this topographical principle).

Cortical topography and the emergent functions

The cortical arrangement of temporal semantic representations and parietal numerical representations suggests that a similar organisational principle might guide how cortical functions transition from a 'segregated and domain-specific' state into an 'integrated and domain-general' state [7]. Specifically, cortical regions surrounding the hub are closer to specific sets of unimodal cortical areas relative to others, both in terms of physical distance and connectivity strength [8]. For instance, the anterior IPS, which is sensitive to finger counting, is closest to and tightly coupled with the somatosensory cortex, whereas the PSPL, which is sensitive to orienting attention along the mental number line, is closest to and intimately linked with the visual cortex. As a consequence of their proximity to the primary sensory

Box 1. Representations versus operations

Both semantic and numerical cognition are multifaceted. In both domains, a multitude of processes can be broadly distinguished into two major dimensions: representations and operations. On the one hand, representations refer to the meaningful contents of semantics or numbers: research has established that semantic meaning and numerical quantity are encoded in the ATL and the IPS, respectively. On the other hand, operations refer to the goal-directed volitional processes performed on the meaningful representations. In semantic cognition, operations can be directed towards selecting particular words to express an intended meaning; in numerical cognition, operations can be directed towards performing arithmetic. Implementing operations entails dissociable neural mechanisms from those of representations, such as additional prefrontal activity (exerting top-down modulatory influences) coupled with ATL/IPS activation. In this article, we discuss how representations are spatially distributed across the cortical sheet, with a specific focus on the topographical similarity between semantics and numbers. In both domains, multiple streams of perceptual processing converge, driving modality-specific representations to emerge in the periphery and supramodal representations in the centroid, which embodies a spatial layout of hierarchical convergence. Although the way in which the brain implements the operations for semantics and numbers is an important issue, it is beyond the scope of the present discussion.

systems (thus, forming immediate connectivity with the nearest sensory cortex), these 'spoke' regions develop their specialisation to process higher-level features from the sensory system they are proximal to. For example, the anterior IPS encodes the bodily schema of fingers, which can be utilised to sustain finger counting, while the PSPL encodes the visuospatial representations of physical space, which can be repurposed to support spatial–numerical associations in an abstract mental space. Multiple lines of unimodal processing eventually converge at some loci, resulting in the emergence of supramodal representations [9]. Critically, the functional heterogeneity of different transmodal hubs might be created by different combinations of modality-related processing that feed into the hub and the anatomical position where the convergence takes place. Specifically, the temporal semantic hub is in the ventral 'what' pathway specialised for recognising the identity of visual/auditory stimuli, whereas the parietal quantity hub is situated in the dorsal 'how' pathway specialised for converting perceptual input to prepare for actions. Constrained by their locus in relation to various unimodal cortices, the emergent representations in the ATL and IPS are used to fulfil different needs. Within the ATL, the representations serve to support visual recognition and verbal comprehension, whereas within the IPS they serve to support numerosity processing that can be generalised across spatial, motoric, and verbal domains. Therefore, from a topographical perspective, although semantic and numerical cognition have long been considered independent faculties, there is a common mechanism that leads to the genesis of ostensibly independent (yet closely interacting) abilities: hierarchical integration across multiple senses, with the surrounding cortical landscape driving their functional divergence.

Concluding remarks

Hierarchical integration happens in parallel in multiple 'local fields' of the brain [7]. Collectively, multiple local hierarchies form a macroscale architecture of **cortical gradient** [8], capturing a progression from sensorimotor functions to transmodal cognition. This macroscale architecture is shared between humans and non-human primates [10]. Instead of contrasting numbers with semantics as diametrically opposed abilities, a fruitful direction in the future would be comparing the similarities and differences of their cortical topography during development, such as longitudinal/sectional investigation into how the acquisition of numerical and linguistic abilities modulate cortical topography over the formative years, as well as testing how cortical topography might be disrupted by developmental or acquired disorders. For example, as semantic/numerical capabilities develop over time, pupils are expected to demonstrate less reliance on sensorimotor strategies (e.g., finger counting) and more efficient extraction of meaning. This maturation process would be mirrored in more activation of supramodal regions and less activation in those sensorimotor regions. This topographical approach might also offer clues as to why macaques and humans develop similar multisensory representations in the parietal lobe for numerosity [11] and in the temporal lobe for audiovisual integration [12]. Such cross-species similarity might be similarly driven by multimodal integration and constrained by the surrounding cortical landscape, potentially applicable to other transmodal functions (e.g., executive control).

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