

## Spotlight

## Task Selectivity as a Comprehensive Principle for Brain Organization

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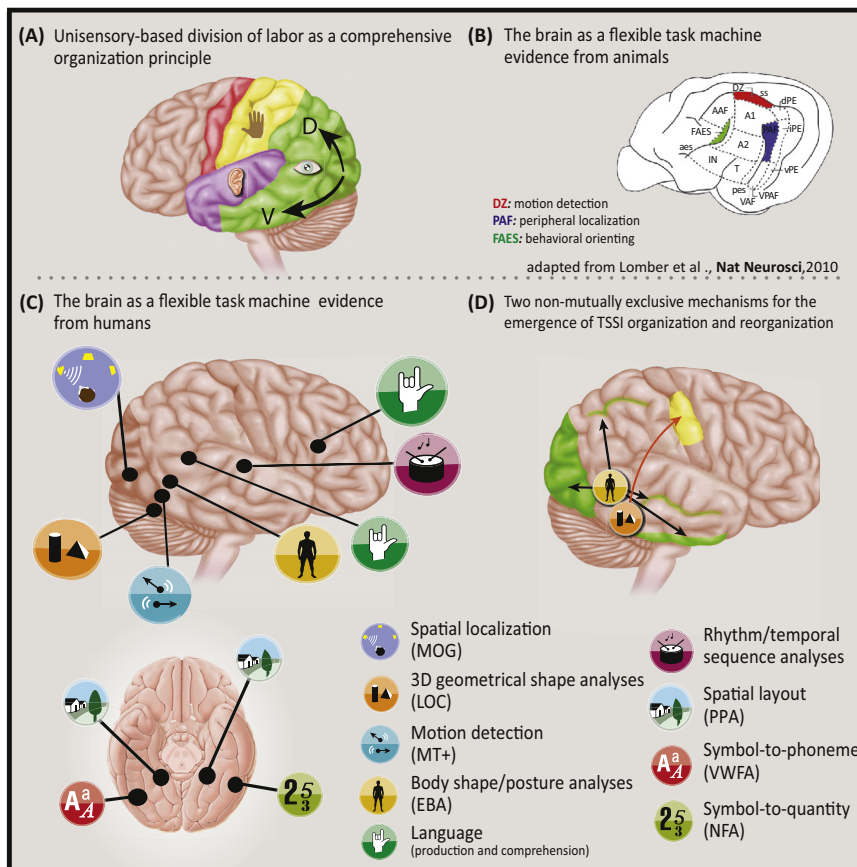
**How do the anatomically consistent functional selectivities of the brain emerge? A new study by Bola and colleagues reveals task selectivity in auditory rhythm-selective areas in congenitally deaf adults perceiving visual rhythm sequences. Here, we contextualize this result with accumulating evidence from animal and human studies supporting sensory-independent task specializations as a comprehensive principle shaping brain (re)organization.**

What underlies the emergence of anatomically consistent specializations in the brain? For many decades, functional brain specializations were considered to arise during evolution through natural selection mechanisms and to be constrained to specific sensory modalities. These assumptions were supported by anatomical consistencies of brain specializations across individuals for the broad sensory division of labor (e.g., visual or auditory regions) and also within specific sensory cortices (e.g., in vision: category selectivity to visual objects, faces, or body images). This constrained account of brain organization was first challenged by the presence of anatomically consistent brain specializations for tasks that were invented too recently for natural selection to occur, such as reading and symbolic arithmetic [1]. These results led to the cognitive neuroscience

theory of ‘neural recycling’, which postulates that sensory cortices can process novel tasks consistently across participants as long as the new task shares basic sensory physical similarities (e.g., shape contours, line conjunctions, and foveal topographic bias for reading-selective brain regions) with the original task processed in that specific brain region [1]. Over the past decade, many studies, conducted for instance with congenitally blind individuals, further challenged the aforementioned dominant view by questioning its core sensory-anchored assumption. They showed that most of the known specialized regions in higher-order ‘visual’ cortices maintained their anatomically consistent category-selective properties in the absence of visual experience when input was provided by other senses carrying category-specific information (reviewed in [2,3]). Some evidence also unraveled the causality of this recruitment for behavior [4]. Preserved category selectivity ranged from the maintenance of the ventral/dorsal ‘visual’ pathways division of labor to specific categories within both pathways, such as localization, motion detection, tools and objects, reading, number identification, and body images, ultimately suggesting that the brain is organized as a task machine rather than as a sensory machine as classically conceived [2,3] (Figure 1C). Several studies reported in the same congenitally blind participants the preservation of functional-connectivity patterns between specific category-selective ‘visual’ regions and other brain regions relevant for that computation [2]. These results led to revision of the neural recycling theory [2,5], which now states that category-selective organization stems from two non-mutually exclusive principles: (i) preservation of large-scale connectivity patterns linking category-selective regions to the whole network involved in a specific task (phonology or quantity networks for letters and numbers processing, respectively); (ii) local computational sensitivity to sensory-independent task-distinctive features

(for reading letters/numbers analyzing the symbols in vision or touch) (Figure 1D), termed task-selective sensory-independent (TSSI) organization. These fascinating studies led to a crucial question: do TSSI organization and its driving principles extend in humans beyond ‘visual’ regions to other high-order sensory cortices?

The recent study by Bola and colleagues [6] provides crucial evidence supporting an affirmative answer to this question, ultimately bridging the gap between humans and animal studies, which had previously already provided affirmative causal evidence in congenitally deaf cats [7] (Figure 1B). Specifically, Bola and colleagues [6] documented auditory cortex recruitment in congenitally deaf and hearing adults when discriminating visual or auditory rhythm sequences, respectively. In both sensory modalities (vision and audition), the activation for rhythm perception peaked in the posterior and lateral part of the high-level auditory cortex, anatomically consistently across subjects (Figure 1C). This suggests that local sensitivity to TSSI features is a principle also characterizing the organization of the high-order human auditory cortex. In addition, the authors [6] observed, through psychophysiological interactions (PPI) analysis, strengthened functional coupling between the rhythm-selective auditory region and the dorsal visual cortex in deaf participants during the visual rhythm discrimination task compared with hearing adults performing the same task either visually or aurally. This highlights the flexibility of connectivity patterns that appear to be capable of adapting their relative strength based on the task demands. This result is especially interesting in the context of recent animal studies documenting largely preserved anatomical connectivity patterns in the auditory cortex of deaf cats [8], suggesting that connectivity biases are present in the auditory cortex similarly to the visual cortex [2,9] (Figure 1D).



## Trends in Cognitive Sciences

**Figure 1. Large-Scale Brain Organization Principles.** (A) The brain as a sensory machine. The classical view dividing the brain into sensory-specific regions (vision, green; auditory, purple; somatosensory, yellow; motor, red). According to this view, in the absence of a specific sensory input (e.g., visual or auditory) during critical periods, the development of brain specializations is expected to be absent or extensively modified. (B) Task-selective sensory-independent (TSSI) brain organization. Evidence for TSSI organization in congenitally deaf cats. Using the reversible cooling of brain regions, Lomber and colleagues causally unraveled the TSSI nature of the deprived auditory cortices of deaf cats by showing that three auditory areas (DZ, PAF, and FAES) maintained their typical task selectivity, albeit the information was conveyed through vision rather than through audition [7]. (C) Overview of the available evidence for TSSI organization in humans (reviewed in [2,3]). Lateral and ventral views of the human brain are depicted. Each icon represents a region that showed activations for the specific task it processes in a sensory-independent manner (spatial localization, 3D geometrical shape analyses, motion detection, etc.), rather than for a specific sensory modality as classically conceived. Anatomical locations are only an approximation. In the lateral view, task selectivity is collapsed across hemispheres. (D) We propose that TSSI recruitment arises from two non-mutually exclusive principles [2], demonstrated here for the perception of body shapes and/or postures and for 3D geometrical shape analyses. For body shape and/or posture analyses, the figure shows that the extra-striate body area (EBA) is selective for processing body shapes and/or postures regardless of the input sensory modality. EBA is functionally connected to other regions known to process body shape and/or posture analyses, such as the posterior superior temporal sulcus (pSTS) and the temporoparietal junction (TPJ) (green areas) [2]. Similarly, for 3D geometrical shape analyses, the figure shows that the lateral occipital complex (LOC) processes 3D geometrical shape identities in a sensory-independent manner [2,3] and is functionally connected to the hand and shoulder areas in S1 (yellow areas; through psychophysiological interactions analysis), which are relevant regions for manipulating and interacting with objects [9]. Adapted from [7] (B).

All these results challenge the classic theory of critical periods, which pairs each category-selective region to a specific sensory modality. Future work could unravel the extent to which the same brain organization principles also apply to the normally developing brain, because results in this direction might diverge

between vision and auditory regions [6,7,9,10]. Furthermore, they should address the natural follow-up question: does TSSI organization extend beyond higher-order cortices to early-sensory cortices, the specializations of which have classically been considered even more strictly constrained to unisensory critical periods and, thus, to a specific sensory modality? Is the entire sensory brain a flexible task machine?

We propose that, to answer this crucial question, special emphasis should be given to topography (e.g., retinotopy or tonotopy), the main large-scale organizational principle of the sensory brain. Such studies might reveal that functional topographic organization is sensory specific and that TSSI organization cannot be extended to early-sensory cortices, ultimately highlighting the existence of constraints in the human sensory brain to specific sensory inputs. This will be in line with results documenting causal task switching towards high-level cognitive functions in the deprived primary visual cortex (V1) [11]. Interestingly, however, recent studies demonstrated the maintenance of the large-scale functional-connectivity patterns characterizing retinotopic and tonotopic biases in congenitally blind [12] and congenitally deaf [13] individuals, respectively, albeit their functional role is still unknown. If specific tasks and/or computations rather than sensory inputs constrain brain specializations, as demonstrated for category selectivity, continuous topographic functional organizations, or at least broad topographic divisions, should emerge in deprived primary regions when using atypical sensory modalities as input. In other words, we suggest that functional topographic organizations might emerge independently of the input used, if the information provided carries core 'retinotopic' (e.g., high versus low shape resolution and spatial position) or 'tonotopic' features (e.g., scalarity and periodicity). This would predict, for instance, the activation of foveal-retinotopic

regions for Braille reading (a task requiring high-resolution shape analyses) in the deprived V1.

Overall, over recent decades, the study of the sensory-deprived brain remarkably modified the notions regarding the origins of brain specializations and the concept of critical periods by highlighting that the emergence of category selectivity is sensory independent in nature. Future work will reveal the extent to which task-selective sensory-independent brain organization is a comprehensive principle of brain organization and how it intertwines with other organization principles to shape brain (re)organization.

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