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Commentary

Neuronal mechanisms enhancing selectivity of the innate number sense via learning

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In their feature article, Lorenzi et al. (2025) compiled extensive biological evidence on the ontogenetic origins of the number sense. Drawing on both behavioral and neurobiological data, they convincingly argue that the "number sense" is fundamentally innate and present from birth in numerically competent animals, including humans. At the same time, the authors acknowledge the role of learning and experience in shaping numerical cognition. This commentary builds on the idea of learning-induced changes to the number sense, extending the concept of an innate number sense to one that is modifiable through learning and experience. It summarizes evidence from single-neuron recordings and proposes neurophysiological mechanisms underlying these learning-induced changes in numerical cognition.

Keywords: learning; number sense; prefrontal cortex; tuning curve; ventral intraparietal sulcus.

Lorenzi et al. (2025) convincingly argue that the "number sense" is innate, but they also acknowledge the role of learning in shaping numerical cognition. A strong argument for learning-induced improvements in numerosity representations comes from a single-neuron recording study in nonhuman primates (Viswanathan and Nieder 2015). In this study, single-neuron responses were examined in two monkeys before and after numerical training. Initially, when the monkeys were in a numerically naïve stage and only discriminated dot colors in dot displays, numerosity-selective neurons were already identified in the ventral intraparietal area (VIP) of the intraparietal sulcus (IPS) and the prefrontal cortex (PFC) (Viswanathan and Nieder 2013)—two core brain regions of the number network in primates (Nieder 2004; Viswanathan and Nieder 2020; Nieder 2025). This provided initial evidence that learning is not required for numerosity-selective neurons to exist in the brain (Viswanathan and Nieder 2013). These neurons respond maximally to a preferred numerosity, with firing rates decreasing systematically for numerosities farther from the preferred one—resulting in a bell-shaped numerosity-tuning function. Similar numerosity-tuned neurons have also been observed in the human brain (Kutter et al. 2018, 2023).

The monkeys of the initial study (Viswanathan and Nieder 2013) were then re-trained to discriminate the number of dots in the displays, and recordings were made in the same brain areas as during the previous naïve condition. After training, PFC showed an increased number of numerosity-selective neurons, which were more selectively tuned to numerosity, exhibiting sharper tuning functions (Viswanathan and Nieder 2015). In contrast, no such improvements were observed in the VIP. The enhanced selectivity of numerosity-selective neurons following numerosity discrimination training reflects perceptual learning, in which numerosity becomes behaviorally relevant for the subject.

Perceptual learning has been extensively studied in the visual system, where it leads to more accurate behavioral discrimination of visual stimuli. This increase in accuracy is associated with narrower tuning curves (Schoups et al. 2001; Yang and Maunsell 2004; Lee et al. 2012). Narrower tuning implies that the neuronal representations of individual neurons overlap less, thereby enhancing neuronal selectivity. In addition to an increase in the absolute proportion of numerosity-selective neurons in the PFC, the numerosity tuning functions became more selective as a result of training and learning (Viswanathan and Nieder 2015). These effects can be explained by at least two distinct mechanisms operating on different time scales during numerosity discrimination: lateral inhibition within local cortical microcircuits enables immediate selectivity adjustments with behavioral relevance, while reinforcement learning, driven by neuromodulator feedback loops, supports long-term changes.

For lateral inhibition to shape tuning curves at the level of local microcircuits, inhibitory interneurons play a crucial role in sharpening the tuning functions of pyramidal cells, the excitatory projection neurons of the cerebral cortex. These two main types of cortical neurons can be distinguished in the primate association cortex based on the waveforms of their action potentials (Merchant et al. 2012). In monkeys trained to discriminate numerosity, inhibitory interneurons were more broadly tuned to numerosity compared to pyramidal cells, providing initial evidence that inhibitory interneurons could sharpen the tuning of pyramidal cells (Diester and Nieder 2008). Moreover, neuron pairs consisting of pyramidal cells and inhibitory interneurons recorded at the same electrode tip, and thus in close anatomical proximity, exhibited inverted tuning to numerosity relative to each other (Diester and Nieder 2008). When these neuron pairs were functionally coupled, as evidenced by temporally correlated discharges, and thus part of a local microcircuit,

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they exhibited systematic connectivity patterns. Neuron pairs consisting of an inhibitory interneuron and a pyramidal cell were functionally connected through a negative correlation in temporal firing, showing inverted tuning relative to each other. In other words, when a putative inhibitory interneuron fired, the connected pyramidal cell was significantly inhibited, and vice versa. Mechanistically, these findings suggest that inhibitory interneurons exert inhibition on numerosity-tuned pyramidal cells (Nieder 2023). Remarkably, the same observation of inverted numerosity tuning in functionally coupled excitatory and inhibitory neurons was made in the differently evolved nidopallium caudolateral of crows (Ditz et al. 2022). This suggests that this type of lateral inhibition in shaping numerosity tuning is not specific to the cerebral cortex but is a general mechanism in the telencephalic pallium of vertebrates.

This lateral inhibition mechanism, which sharpens neurons' numerosity tuning, becomes enhanced with monkeys' proficiency in discriminating numerosity, but in an area- and neuron-type-specific manner. In the VIP, neither pyramidal cells nor inhibitory interneurons showed sharpened numerosity-tuning functions as a result of learning (Viswanathan and Nieder 2015). These findings suggest that numerosity is rapidly and automatically encoded in a bottom-up fashion in VIP, regardless of task demands, supporting the idea of an innate number sense. However, in the PFC, pyramidal cells showed increased numerosity selectivity after training, whereas interneurons remained unaffected (Viswanathan and Nieder 2015). This improved selectivity may enable the PFC to exert top-down influence on downstream cortical areas, guiding executive functions through numerical information.

In the PFC, not only do numerosity-selective neurons become sharper, but the proportion of numerosity-selective neurons also increases slightly with learning. This suggests that originally untuned neurons are converted into tuned neurons over the course of long-term learning. Similarly, when monkeys are trained to discriminate arbitrary categories, such as cats versus dogs or categories of visual motion directions, neurons in the prefrontal and posterior parietal cortices reflect the category membership of visual stimuli, with their selectivity shifting when stimuli are retrained into new categories (Freedman et al. 2001; Freedman and Assad 2006). This effect—the emergence of newly category-tuned neurons—can be explained by reinforcement learning. According to a cortical circuit model, weak but systematic correlations between trial-to-trial fluctuations in firing rates and the accompanying reward following appropriate behavioral choices lead neurons, even initially nonselective ones, to gradually become category-selective (Engel et al. 2015). In the number domain, this mechanism may help explain why more numerosity-selective neurons are present as a subject learns to respond appropriately to numerosity in order to receive a reward.

The comparison of single-neuron data in monkeys trained on different visual categories suggests that learning-dependent neuronal plasticity in the primate association cortices is specific, and more precisely, limited to numerical categories. In stark contrast to the dramatic categorical coding changes observed in the IPS for arbitrary perceptual categories (Freedman and Assad 2006), such changes were absent for number categories. Numerosity representations in the primate association cortex rely on a sparse code with stable "labeled lines" (Nieder and Merten 2007; Moskaleva and Nieder 2014). The rapid and automatic encoding of numerical categories in VIP, without learning-dependent improvements, suggests pure bottom-up processing, consistent with the idea of an innate number sense. However, the number system in the primate brain is also enhanced by learning and experience throughout life, a process that can be explained by the learning-dependent improvement of PFC neurons, which then exert top-down influences on upstream brain areas. While the number sense is fundamentally innate, empirical influences also play a role in numerical cognition and can be traced down to the level of single neurons.

Author contributions

Andreas Nieder (Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing—original draft, Writing—review & editing).

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