Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Basic Mechanisms of Numerical Processing: Cross-Modal Number Comparisons and Symbolic Versus Nonsymbolic Numerosity in the Intraparietal Sulcus

Christina F. Chick
Department of Human Development Graduate Program, Cornell University, Ithaca, New York 14853
Review of Cappelletti et al.

The most basic form of numerical cognition is numerosity, which is the ability to discern the quantity of objects in a set (e.g., are there more blue dots or more yellow dots?). Numerosity is considered part of an evolutionarily ingrained approximate number system, which supports estimation of quantities without the use of symbols (e.g., Arabic numerals) or language. The approximate number system has been observed in human babies, nonhuman primates, and even birds and fish (Knops and Willmes, 2014). Building on this common ground, scholars debate the extent to which a common mechanism supports numerosity and other quantitative judgments, such as estimates of time and distance (Bueti and Walsh, 2009), and the extent to which the approximate number system is separate from abstract mental arithmetic (e.g., math problems expressed as Arabic numerals). Regarding the second debate, on the one hand, there is evidence of considerable behavioral and neural overlap between approximate and abstract numerical processing (Knops and Willmes, 2014). On the other hand, multiple studies have demonstrated dissociations between symbolic and nonsymbolic numerical processing (Lyons and Beilock, 2013).

In a recent article in *The Journal of Neuroscience*, Cappelletti et al. (2013) reported results that speak to both of the debates described above. First, the authors demonstrated that improvements in numerosity after training can transfer across domains, from basic quantity comparisons (trained task: are there more blue or yellow dots?) to judgments about time (untrained task: which time interval was longer?) and space (untrained task: which line is longer?). Further, they demonstrated that the skills underlying this transfer rely on the intraparietal sulcus (IPS)/posterior parietal cortex (PPC), an area that has been consistently found to support both symbolic and nonsymbolic number processing (Hauser et al., 2013). Training-based improvements transferred to untrained quantity discrimination tasks only when the training was accompanied by transcranial random noise stimulation (tRNS) applied to the IPS/PPC. Training accompanied by sham tRNS or by tRNS applied to motor regions did not transfer to untrained tasks, nor did tRNS without training improve task performance. Crucially, numerosity improvements resulting from the combination of training and tRNS applied to the IPS/PPC did not transfer to untrained arithmetic problems, suggesting that nonsymbolic number processing (e.g., continuous quantity judgments) is at least partially dissociable from abstract number processing (e.g., mental arithmetic). These results are consistent with the theory that different types of magnitude information (e.g., quantity, time, and space) share processing resources, including common neural substrates in the IPS/PPC. In addition, they indicate the existence of behavioral and neural dissociations between symbolic and nonsymbolic number processing.

Two methodological strengths make this study important to the characterization of the approximate number system. First, the design ruled out alternative explanations that have limited other studies on this topic. Other studies of numerosity transfer, for example, have confounded gains in numerical discrimination with enhancement of more general cognitive processes, such as working memory and attention. In contrast, Cappelletti et al. (2013) tested for transfer to tasks measuring arithmetic skills, visual pattern recognition, and executive function, in addition to tasks hypothesized to share the trained mechanism of quantity estimation (namely, judgments of time and space). The selective transfer of visual quantity discrimination training to other forms of quantity estimation is evidence that these basic numerosity judgments share a mechanism that does not fully account for more abstract cognitive processes (Price et al., 2012). In addition, the lack of cognitive transfer in control conditions, including sham tRNS and stimulation of the motor cortex, supports the conclusion that the numerosity transfer associated

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Correspondence should be addressed to Christina F. Chick, Human Neuroscience Institute and Cornell Magnetic Resonance Imaging Facility, G331 Martha van Rensselaer Hall, Cornell University, Ithaca, NY 14853. E-mail: cfc53@cornell.edu.
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with tRNS was specific to stimulation of the IPS/PPC.

The second methodological strength is the use of tRNS, which supports the inference that the stimulated parietal regions were necessary to the transfer of quantification skills. tRNS is thought to increase synaptic plasticity by depolarizing the membrane resting potential of targeted brain regions, allowing repolarization to be speeded by the application of random excitation pulses (Fertonani et al., 2011). This putatively increases neuronal excitability, augmenting the benefits of cognitive training (Terney et al., 2008). Whereas most functional neuroimaging studies manipulate stimuli or behavior and observe associated changes in neural activation, tRNS and a family of related brain stimulation techniques manipulate activation in a targeted brain region to test hypotheses about the necessity of that region to a behavior of interest (Miniussi et al., 2013). Many anatomical regions have a high base rate of activation across dissimilar tasks, and although a region may contribute to multiple cognitive processes, demonstrating the necessity of that region to any of those mental processes is difficult due to the correlational nature of fMRI (Poldrack, 2011). Brain stimulation techniques such as tRNS circumvent this problem by manipulating activation in a targeted region, thereby testing the necessity of that region to the cognitive process of interest.

One limitation of tRNS research is that it does not identify the broader network of nonstimulated regions that contribute to task performance; nor does it provide information about the timing or sequence of neural events leading up to the observed outcome. However, experiments using other techniques augment the current findings. For example, an accumulator–comparator model of the IPS, as demonstrated in sensory and probabilistic decision making, may also characterize the role of the IPS in numerosity judgment. The IPS accumulates perceptual evidence, such that visual, auditory, or tactile inputs are collected until they exceed a threshold (Usher and McClelland, 2001; Heekeren et al., 2008). The IPS has also been implicated in an accumulator–comparator model of probabilistic decision making. For example, Gould et al. (2012) used transcranial magnetic stimulation (TMS) to temporarily disable the IPS. By manipulating activation in this region, they showed that the IPS integrates evidence toward one of two competing decision thresholds. Similarly, Hunt et al. (2012) reported that the lateral IPS activated in proportion to the difference in value between two options. Finally, Basten et al. (2010) found that activation in the middle IPS was higher for decisions with smaller cost–benefit differences, consistent with an accumulator–comparator function for the IPS.

Based on these studies of perceptual discrimination and probabilistic decision making, the IPS appears to integrate multiple quantitative inputs into a comparative output signal by accumulating evidence toward a decision threshold. To the extent that basic mechanisms of quantity estimation are shared across dimensions, including number, time, and probabilistic outcome tracking, the accumulator model is a plausible mechanism for the categorical numerosity discrimination tasks used by Cappelletti et al. (2013). Accordingly, Dormal et al. (2012) argue that both numerosity judgments of dot arrays and duration judgments of time intervals are jointly supported by an accumulator in the IPS.

Beyond the plausibility of the accumulator model in explaining numerosity judgments, the findings reported by Cappelletti et al. (2013) are consistent with other recent reports of shared mechanisms for numerical and temporal judgments. For example, Hayashi et al. (2013) showed a congruency effect between judgments of numerical magnitude (in the form of numerals and dot arrays) and perceptions of the duration of a visual stimulus. When the numerals or dot arrays represented larger quantities, participants perceived the visual stimulus as having been presented for a longer time. Moreover, TMS disruption of the IPS enhanced the congruency of numerical magnitude with perceived stimulus duration, suggesting that perceptions of numerical and temporal magnitudes interact in the IPS. Dormal et al. (2012) also found that the same area of the IPS was active during numerosity judgments (i.e., flashed dot sequences) and duration judgments (i.e., the duration of single dot displays). These studies are consistent with Cappelletti et al. (2013) in suggesting a shared mechanism for time and number processing, supported by the IPS.

However, further study of the role of the IPS in cross-modal numerical discrimination must resolve inconsistencies between the results reported by Cappelletti et al. (2013) and those in other published work. The apparent dissociation between approximate numerosity and abstract number processing is particularly controversial. For example, Hauser et al. (2013) applied transcranial direct current stimulation (tDCS) to the IPS/PPC, which temporarily increased activation in this region. tDCS enhanced both magnitude processing and mental arithmetic, demonstrating a role for the IPS in both functions. Hauser et al. (2013) stimulated areas P3 and P4, the same regions stimulated by Cappelletti et al. (2013). That stimulation of the same regions enhanced both numerosity and arithmetic in one study but not in the other underscores that the role of the IPS in approximate and abstract numerical judgments remains to be precisely characterized.

The partial dissociation between approximate and abstract number processing, and the inconsistent effects of IPS stimulation on arithmetic calculations, might be explained by cooperation between frontal and parietal regions during more abstract numerical processing. As Cappelletti et al. (2013) note, it is possible that both frontal and parietal regions would need to be stimulated in order for numerosity training to transfer to abstract arithmetic. Cooperation between frontal and parietal regions during higher-level numerical processing could explain how abstract numerosity builds upon the basic mechanisms of approximate numerosity. There is clear evidence of frontoparietal cooperation during accumulation and comparison, particularly in more abstract comparisons. For example, Knops and Willmes (2014) found that a network including the IPS and inferior frontal cortex was activated both while subjects judged whether Arabic numerals were listed in ascending order and while they solved arithmetic problems. Dormal et al. (2012) also report functional connectivity between the IPS and frontal regions during both numerosity judgments of flashed dot sequences and duration judgments of single dot displays, indicating that frontoparietal cooperation sometimes characterizes even approximate numerical judgments.

In summary, Cappelletti et al. (2013) implicate the IPS in cross-modal numerosity discrimination by showing that the combination of training and tRNS stimulation of the IPS supports transfer of improved performance on a trained numerosity task (comparing sets of dots) to untrained tasks that also require judgments of continuous quantities (along the dimensions of time and space). Notably, this transfer did not extend to untrained tasks requiring mental arithmetic or to more general cognitive capacities, such as attention or working memory. These results speak to two debates within the numerosity literature. First, they support a model of generalized magnitude representation, such that the IPS subserves multiple quantitative dimensions, including time and space (consistent with an accumulator–comparator model of IPS function; Bueti and Walsh, 2009). Second, the results show dissociation between approximate numerosity and symbolic arithmetic, possibly due to increased cooperation between frontal and parietal regions during the latter more abstract process. Further research addressing these controversies will benefit from the use of careful experimental controls and tools such as tRNS, which, in combination, support causal inferences that distinguish among competing cognitive process theories.

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