2010*b*). I suggested that the invention of the clay-token system offered a "material scaffold" able to objectify and simplify the problem of number and thus to restructure the cognitive task needed for its solution. This restructuring may have forged an extended reorganization in the neural connectivity of the critical intraparietal areas associated with numerosity. In other words, the tangible material reality of the clay token—as an "epistemic" artefact (Kirsh 1995)—made possible that the parietal system, previously evolved to support numerosity, gets reorganized and thus partially "recycled" to support the representation of exact number (cf. Piazza and Izard 2009).

The above hypothesis, I think, is consistent and complementary with much that is being proposed by Coolidge and Overmann, especially in terms of the neurological network of numerosity and the links with metaphorical thinking. Where our views seem to diverge nonetheless is in how we perceive the role of material culture in the development of numerical thinking. The "internalist" foundation of Coolidge and Overmann's model allows that material culture can only be seen as a passive externalization device. On this construal, the clay token may well facilitate or provide the stimulus for the expression of number, but the mental process that *really matters* is realized in neural tissue and localized somewhere in the parietal regions of the brain. In other words, for Coolidge and Overmann the process responsible for the development of numerical and symbolic thinking takes place inside the head (but see Overmann, Wynn, and Coolidge 2011). I propose instead that this process extends beyond skin and skull and would have been impossible to achieve by the unaided biological brain. In fact, I argue for the ontological priority of material engagement in the emergence of abstract thinking and symbolic number. What this claim holds, put simply, is that the material instantiation of the concept of number must precede or coemerge with its neural instantiation. From such an enactive perspective, finger counting, engraved marks, or clay tokens do more than simply *stand for* number: they *bring forth* the number (Malafouris 2008, 2010*a*).

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Coolidge and Overmann have gathered an impressive amount of material from disparate areas such as semiotics, developmental psychology, neurobiology, and archaeology. Particularly inspiring are their views about the putative cognitive factors motivating analogical reasoning and metaphoric thinking in us humans. Here, I would like to take a slightly different stance on what it means to understand symbols. Reviewing neurobiological evidence, I will arrive at the conclusion that the PFC, not the parietal cortex, endows *Homo sapiens* with symbolic thinking.

In the target article, the term "symbol" (and thus "symbolic thinking") is used for all sorts of associations between a signifier and a signified. This is problematic because not all referential associations need to be symbolic. Referential associations can adopt different levels of complexity (Deacon 1997; Peirce 1955), from icons (reference based on similarity) and indexes (reference based on contiguity or correlation) to symbols (arbitrary signs embedded in a referential system). Symbolic reference is crucially a link between sign-sign relations, not between individual sign-object relations. As a consequence, only symbols can be manipulated on the basis of compositional rules (i.e., syntax). When evaluating the emergence of symbolic thinking in *H. sapiens*, this distinction becomes essential because only symbolic reference distinguishes humans from animals. Iconic (tally sticks, finger counting, shell beads) and indexical (shape-quantity associations) representations of cardinality can also be mastered by animals (Diester and Nieder 2007), but such representations do not progress on to the level of symbols. Evidence for iconic stages can be found both in human history and in children's acquisition of numbers (Wiese 2003). Children, however, rapidly transcend this stage, and numerical competence in humans passes from an iconic to an indexical and finally symbolic stage. This is the striking discontinuity that needs to be explained during human evolution.

Which brain area allows us to establish semantic associations to ultimately arrive at a symbol system? The authors advocate the parietal lobe, and the IPS in particular, as the key structure for the emergence of symbolic thinking. The IPS is surely a core structure for the representation of semantic aspects of numerical quantity (Nieder and Dehaene 2009; Nieder, Diester, and Tudusciuc 2006). However, neurobiological evidence suggests that the (granular) PFC may fulfill the requirements necessary for high-order associations between signs, ultimately giving rise to the cultural invention of linguistic and number symbols (Nieder 2009). This development can be witnessed both phylogenetically (in nonhuman primates) and ontogenetically (in human infants).

Diester and Nieder (2007) trained rhesus monkeys to associate the shapes of Arabic numerals with the numerosity of dot patterns ranging from 1 to 4. Only in the PFC, but not in the IPS, many of the same neurons were equally active to the numerical values assigned to the numeral shapes. Thus, in nonhuman primates, both prefrontal and parietal neurons represent numerical values, but unlike parietal neurons, only prefrontal neurons have the additional capacity to associate numerosity and an Arabic numeral shape as its indexical referent. These findings suggest the PFC as the prime phylogenetic source in the mapping process of initially meaningless shapes to semantic categories, giving rise to an indexical understanding of signs. Support for this assumption comes from recent fMRI studies with children. When comparing numerical values in symbolic (numerals) and nonsymbolic notation (sets of dots), children at the ages of six and seven invoke the same cortical networks previously described for adults, with parietal brain regions as key structures. Interestingly, however, children also recruit the inferior frontal cortex (granular frontal cortex BA 44/45) for notation-independent numerical processing to a much greater degree than adults (Cantlon et al. 2009; Kaufmann et al. 2006). Similarly, a greater engagement of frontal brain regions during Arabic numeral judgments (Ansari et al. 2005) and symbolic arithmetic tasks (Rivera et al. 2005) has been described in children compared with adults. These results point to the PFC as the cardinal structure in acquiring a symbolic number concept during ontogeny. Only with age and proficiency, the activation seems to shift to parietal areas.

Coolidge and Overmann concentrate on semantic aspects of symbol systems. However, to establish a full-fledged symbol system, meaningful sign-object associations must be accompanied by rules guiding the structuring of signs (syntax). Syntax and semantics of individual sign-sign relations are inextricably linked. Such circuitry representing rules is also hosted by the PFC. In monkeys required to flexibly switch between "greater than/less than" rules, Bongard and Nieder (2010) have recently shown that the activity of single neurons reflected these abstract numerical rules. We speculate that these neuronal circuits in the monkey lateral PFC could readily have been adopted in the course of primate evolution for syntactic processing of numbers in formalized mathematical systems. The collected empirical evidence argues that the network of the PFC, not the parietal cortex, endowed us humans with full-fledged symbolic thinking.

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Coolidge and Overmann discuss the neurological substrate of numerosity processing because it is one of the a priori conditions for numerosity processing to play a role in the development of the abstraction capacity. In this description they make two inappropriate assumptions that are unfortunately very frequently made, even by researchers in the field. First, they consider the brains of monkeys and humans to be highly similar and presume that anatomical regions such as the IPS correspond functionally in the two species. The human brain is much larger than that of monkeys: the human cortical surface is about 10 times that of monkeys. The two species, which diverged over 23 MYA, exhibit quite different behaviors, and it therefore is not surprising that at least in some respects the brains of the two species differ significantly. One such instance is the inferior parietal cortex, which is greatly expanded in humans (Van Essen and Dierker 2007). As a consequence, human cortical regions corresponding to monkey regions located in the IPS have moved dorsally and are located in the medial wall of the human IPS or even in the adjacent superior parietal lobule (SPL; Durand et al. 2009; Grefkes and Fink 2005). In the monkey, numerosity-selective neurons are located in the ventral intraparietal area (Nieder and Miller 2004), and their human counterparts should therefore be located in the SPL. The second point of confusion is between recording single neurons and fMRI. The latter technique measures a hemodynamic response in so-called voxels, which are typically a few millimeters on a side and include millions of neurons. Given the pooling of so many neurons, it is difficult for fMRI to quantify the main property of single neurons in that sample: their selectivity for a functional aspect of the stimulus, here numerosity. Indirect techniques, such as repetition suppression or multivoxel analysis, have been devised to circumvent these limitations, but with only limited success (Sawamura, Orban, and Vogels 2006). A meaningful relationship between single neurons recorded in monkeys and fMRI data obtained in humans can, however, be established using monkey fMRI as a linking technique (Orban 2011).

In their discussion concerning the abstraction of numerosity, the authors describe two processes: linking a sensory (e.g., visual) representation of a number of objects to a symbol (the number) and relating ordered sequences of numbers to sequences of other symbolic entities such as days or months. The latter process has a higher chance of being typical of the human lineage. Indeed, Diester and Nieder (2007) have shown that by training monkeys, prefrontal neurons may acquire selectivity for abstract symbols that have been associated with visual quantities through training. After training, prefrontal neurons exhibit selectivity for a given numerosity and for the symbol associated with it by training. In their study, Diester and Nieder (2007) found very few parietal neurons with this combined selectivity. It is, however, possible that with training at an earlier age, such parietal neurons may be observed in the monkey parietal cortex. Therefore, we should consider the possibility that the first step in abstracting numerosity is shared with nonhuman primates. The second step in the abstraction process, generalization across different types of ordered sequences (Fias et al. 2007), remains more likely a typically human achievement, although here also it is difficult to assess which of our ancestors possessed this capacity.

When discussing changes in the parietal lobe during the evolution of our species, the authors quote our studies demonstrating that functional properties of parietal regions have changed during evolution (Orban et al. 2006; Vanduffel et al. 2002). In particular, we have shown that sensitivity to motion and to three-dimensional shape extracted from motion is stronger in the human than in the monkey parietal cortex. In those studies, we suggested that some of the functional differences in the parietal lobe may be related to tool use, which is much more developed among humans than in nonhuman primates. Recently, we provided direct evidence for a parietal region involved in understanding tool use that is present in humans but not monkeys (Peeters et al. 2009). Tools have the advantage that their development can be traced in the archeological record. Using this record, we speculated that this parietal area was perhaps present in *Homo erectus*, to whom the Acheulian in-

in the abstraction process (or higher-level abstraction) may be unique to modern humans. Finally, our extension of the dual systems of numerosity as a tentative foundation for humans' intuitive penchant for analogies and metaphors not only remained unscathed in the commentaries but untouched; we look forward to future dialogue on this part of our argument, as a recent book (e.g., Geary 2011) has highlighted the ubiquitousness of metaphors and their centrality to modern thinking. As Geary provocatively yet cryptically noted in his foreword, "Metaphor is a way of thought long before it is a way with words" (Geary 2011:3), which is completely consonant with our central thesis.

—Frederick L. Coolidge and Karenleigh A. Overmann

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