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Numerical representation in the parietal lobes: Abstract or not abstract?

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Abstract: The study of neuronal specialisation in different cognitive and perceptual domains is important for our understanding of the human brain, its typical and atypical development, and the evolutionary precursors of cognition. Central to this understanding is the issue of numerical representation, and the question of whether numbers are represented in an abstract fashion. Here we discuss and challenge the claim that numerical representation is abstract. We discuss the principles of cortical organisation with special reference to number and also discuss methodological and theoretical limitations that apply to numerical cognition and also to the field of cognitive neuroscience in general. We argue that numerical representation is primarily non-abstract and is supported by different neuronal populations residing in the parietal cortex.

Keywords: abstract; automaticity; brain; cognition; neuronal specialisation; numbers; parietal lobes; prefrontal cortex; representation

1. Introduction

In today's high tech society, numbers play a central role. We use them to calculate budgets, compare prices, understand food labels, and discuss journal impact factors. Not surprisingly, difficulties in handling numerical information can lead to serious impairments in everyday life (Ansari 2008; Butterworth 1999; 2004; 2005; Cohen Kadosh & Walsh 2007; Parsons & Bynner 2005; Rubinsten & Henik 2009; von Aster & Shalev 2007). Numbers can come in many forms; we can represent the same quantity, say "two" (here a word) as a digit (2), in Roman numerals (II), non-symbolically as on a dice (⁘), with our fingers, in a temporal series (e.g., a drum beat), or with other words (pair, duo, brace) that carry semantic as well as numerical meaning. The question of how we represent numbers and whether there is a unitary neuronal basis for all forms of numerical representation is therefore important. A full understanding of numerical representation is also important for the correspondence between comparative and developmental studies that use non-symbolic representation and studies in adults that can use symbolic and non-symbolic stimuli. Moreover, insights into the way we represent numbers are proving to be important for educational interventions, for diagnosis, classification, and the design of effective rehabilitation programs for people who suffer from numerical difficulties known as developmental dyscalculia. For example, the way in which some intervention programs are designed in order to help children with dyscalculia (Wilson et al. 2006a; 2006b) is based on the idea of abstract representation. Therefore, it is assumed that training on numerosity will improve the numerical computation with digits.

2. The consensus

Over the last ten years a consensus view has emerged that assumes the underlying representation of numerical information to be abstract and to be focussed in the intraparietal sulcus (Dehaene et al. 1998). Here we reassess this abstract representation point of view. By abstract we adopt the previous operational definition (Dehaene et al. 1998, p. 356) that "Adults can be said to rely on an abstract representation of number if their behavior depends only on the size of the numbers involved, not on the specific verbal or non-verbal means of denoting them." (See also McCloskey, 1992, p. 497, for a similar definition.) Other, more recent studies, support this view and point out that "the intraparietal sulcus (IPS) as an important region for numerical cognition ... represents number regardless of whether the input notation is symbolic (e.g., number words or symbols) or non-symbolic (e.g., dot patterns) and regardless of whether stimuli are presented visually

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or auditorily" (Libertus et al. 2007, p. 2). Therefore, an operationalization of abstract representation in the present article is that neuronal populations that code numerical quantity are insensitive to the form of input in which the numerical information was presented (e.g., digits, verbal numbers, auditory, numerosity, etc.). In contrast, we define non-abstract representation as neuronal populations that code numerical quantity but are sensitive to the input in which the numbers were presented. Therefore, the neuronal populations that code the magnitude of the digit 7, or the word "SEVEN" will not be identical. However, the expected output for abstract and non-abstract representations is similar. For example, for both representations we know that 7 is larger than 6, and SEVEN is larger than SIX. Nevertheless, we will show here that non-abstract representation can be masked as a function of the response made by subjects and that detecting differences between different notations are optimised by probing automatic processing. Such a difference cannot be explained if the same neuronal population codes numerical quantity independent of the input.

There are several ways to define representation (for reviews, see Barsalou 1999; 2003; Markman & Dietrich 2000), but in this target article we define representation only in the general sense that is most common in psychology and cognitive neuroscience. Here representation refers to patterns of activation within the brain that correspond to aspects of the external environment (Johnson & Munakata 2005). We differentiate representation from processing; the latter includes representation, but relates to the sum of pre-representation (e.g., visual identification of the digit) and post-representation components (e.g., working memory, response selection). In the current case numerical representation relates to patterns of activation that are modulated by the numerical magnitude conveyed by the number.

We suggest in this review that the commonly held view of abstract numerical representation needs to be challenged; we present evidence supporting a contrary view, and provide future directions for empirical work in cognitive and developmental neuroscience.

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Vincent Walsh is Professor of Human Brain Research at University College London. Among his research interests are higher visual perception, time perception, and numerical cognition. He has forwarded the idea that time, space, and number mechanisms draw on evolutionary and developmentally common resources ("A Theory of Magnitude" in *Trends in Cognitive Science*, Vol. 7, No. 11, 2003) as a means of explaining the emergence of number in a brain region concerned with sensory motor transformations. Recently, he has begun to work on real scene perception and also the role of sleep in learning and cognition.

3. Architectures for number processing

Models of number processing differ with respect to the issue of whether numbers are abstractly represented. There are many cognitive models in the field of numerical cognition (e.g., Cipolotti & Butterworth 1995; Gallistel & Gelman 1992; Noël & Seron 1993; 1997; Pillon & Pesenti 2001; Schwarz & Ischebeck 2003), but three central models are the most cited and are representative of the key features of different classes of models.

McCloskey and colleagues in a series of neuropsychological studies (e.g., Macaruso et al. 1993; McCloskey et al. 1985; Sokol et al. 1991) have shown that a single, abstract representation can provide detailed qualitative and quantitative accounts of the errors made by acalculics (patients with acquired numerical difficulties). These findings led McCloskey (1992) to offer the *abstract modular model* that is composed of three distinct parts: the comprehension system, the calculation system, and the number production system. The comprehension system converts different notations of numbers (e.g., digit, verbal numbers, roman, etc.) into a common abstract format. The calculation system includes arithmetic facts such as the comparison task and calculation procedure, both of which are also a form of abstract quantity code. The production system produces the output in various notations as requested, such as digits, or spoken numerals. An important assumption in McCloskey's model is that an abstract internal representation carries out all numerical operations. This implies that all inputs, without exceptions, are converted into a single, modality-independent abstract representation and then are translated into the appropriate form of output. Consequently, the pattern of reaction times (RTs) between digits, verbal numbers, or any other symbolic notation should follow predictions based on abstract coding, because they are translated into one common representation. A general difference among the overall mean RTs might appear because of different processing times of different notation inputs (e.g., digits are responded to more quickly than roman numerals). However, an important prediction that follows from abstract coding is that there should not be RT interactions between the different notations. Rather, the abstract coding model predicts additivity between different numerical notations when one manipulates factors which influence the level of numerical representation.

While McCloskey's model strongly posits abstract representation, Campbell and colleagues (Campbell 1994; Campbell & Clark 1988; Campbell & Epp 2004) have suggested that numbers are not represented abstractly. According to their *encoding complex hypothesis*, separate modality-specific number codes exist. Therefore, number processing is mediated by modality-specific processes (e.g., visual, digit) and not by an abstract code. Consequently, they predict RT interactions between responses

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to numbers as a function of notation or stimulus modality. More precisely, they do not predict any additivity between different numerical notations; rather, they predict an interaction between notation and factors that are influenced by the numerical representations.

Dehaene (1992) combined features of the abstract modular model and the encoding complex hypothesis and composed the currently most accepted cognitive model: the *triple-code model*. Similar to the encoding complex hypothesis, this model does not assume a single central number representation. Instead, it assumes that there are three different codes with special and distinct functions for each. The first two codes are modality- and notation-dependent; The Arabic code, which resides in the left and right inferior ventral occipital-temporal areas, is responsible, for example, for multi-digit calculations. Simple calculations, verbal counting, and retrieval of arithmetic facts are executed via a verbal code, which is subserved by the left perisylvian area. However, numerical comparison and number approximation, which access the numerical representation, are performed using the third code, the analogue magnitude code, in which the representation, as in McCloskey's model (1992), is modality- and notation-independent. Hence, it is possible to find notation-dependent processing for arithmetic operations resulting from non-representation–related processes outside the analogue magnitude code (e.g., verbal code), while the numbers in the equation are represented abstractly by the analogue magnitude code. Therefore, this model, like the abstract modular model, predicts additivity between different numerical notations when one manipulates factors that influence the level of numerical representation. This idea was mentioned in several later works, for example, in Dehaene (1996) where the author writes "the same representation of number magnitudes should be accessed regardless of input number notation" (p. 60). In later works, which marked the transition of the abstract view from a purely psychological concept to a neurally instantiated one, it was stated that the IPS codes the abstract, rather than non-abstract, quantity meaning. For example, after reviewing neuroimaging studies, Dehaene and colleagues concluded that, "Those parametric studies are all consistent with the hypothesis that the HIPS [horizontal IPS] codes the abstract quantity meaning of numbers rather the numerical symbols themselves." (Dehaene et al. 2003, p. 492).

4. Numbers are abstract

The logic behind the idea that numbers are represented in an abstract fashion can be examined in a straightforward way. If numerical representation is abstract, then the representation-related effects caused by one type of notation or modality should be identical for other notations or in other modalities. That is, the effect for each notation or modality should be additive, rather than interacting with the notation. Such effects have been observed for a variety of notations and modalities both at the behavioural (e.g., Barth et al. 2003; Dehaene & Akhavein 1995; Naccache & Dehaene 2001b; Schwarz & Ischebeck 2000) and the neuronal level (e.g., Dehaene 1996; Eger et al. 2003; Libertus et al. 2007; Naccache & Dehaene 2001a; Pinel et al. 2001), thus supporting the idea that numbers are represented abstractly. The spatial numerical association of response codes (SNARC) effect is a classic example; subjects respond more quickly to small numbers with left-hand key responses than with right-hand key responses, and faster to large numbers with the right-hand key than with the left-hand key (e.g., responding to digit 3 will be faster with the left-hand key, whereas responding to digit 8 will be faster with the right-hand key) (Dehaene et al. 1993; Fias & Fischer 2004; Gevers & Lammertyn 2005; for a recent meta-analysis see Wood et al. 2008). The effect is independent of notation or modality (Nuerk et al. 2005; see also our Figure 1a). Similarly, in the numerical distance effect, RT increases as the numerical distance between two numbers decreases (e.g., RT to decide if 8 is larger than 2 is faster than RT to decide if 8 is larger than 6) (Moyer & Landauer 1967). This effect too, by and large, is independent of notation (Dehaene 1996; Dehaene & Akhavein 1995; Naccache & Dehaene 2001b; Schwarz & Ischebeck 2000) (see our Figure 1b). These and other cognitive effects gave support for the triple code model (Dehaene 1992). Extrapolating the idea of abstractness from this cognitive model (Dehaene 1992) to the nervous system implies that within the IPS, the area most associated with numerical representation (see Cohen Kadosh et al. 2008f; Dehaene et al. 2003, for reviews and meta-analyses), the same neural population will be recruited to encode numerical quantity, whatever the format of presentation. Neuroimaging experiments have reported notation- and modality-independent brain activation in the IPS (Eger et al. 2003; Naccache & Dehaene 2001a; Pinel et al. 2001; see also Venkatraman et al. 2005, for evidence of format-independent processing of exact and approximate arithmetic in the IPS) (see our Figure 1c). Together these findings, both at the behavioural and the neuronal level, provide an apparently strong basis for the abstract representation of numbers. However, there are several limitations to this view.

5. Numbers are not abstract

Despite the evidence presented in the previous section, the logic behind the assumption that numbers are represented in an abstract fashion is incomplete and suffers both from methodological and theoretical shortcomings. While it is true that different notations/modalities can yield similar behavioural effects, it does not follow that they therefore share a single neuronal representation. It is entirely possible, for example, that similar behavioural effects can be subserved by different brain areas, or neuronal populations in a single brain area, and in different time windows (Cohen Kadosh et al. 2007a; Rumelhart & McClelland 1986). It is also often overlooked that, at the behavioural and neural levels, the assumption that numbers are represented in an abstract fashion is based mainly on null results, that is, on finding no differences between notation or modality and the behavioural or blood oxygenation level dependent (BOLD) variable that correlates with numerical representation. Therefore, the conclusion that numbers are abstract may be due to a lack of statistical power, or the insensitivity of the paradigms used. Indeed, some studies *have* found differences or a tendency towards a difference between notations

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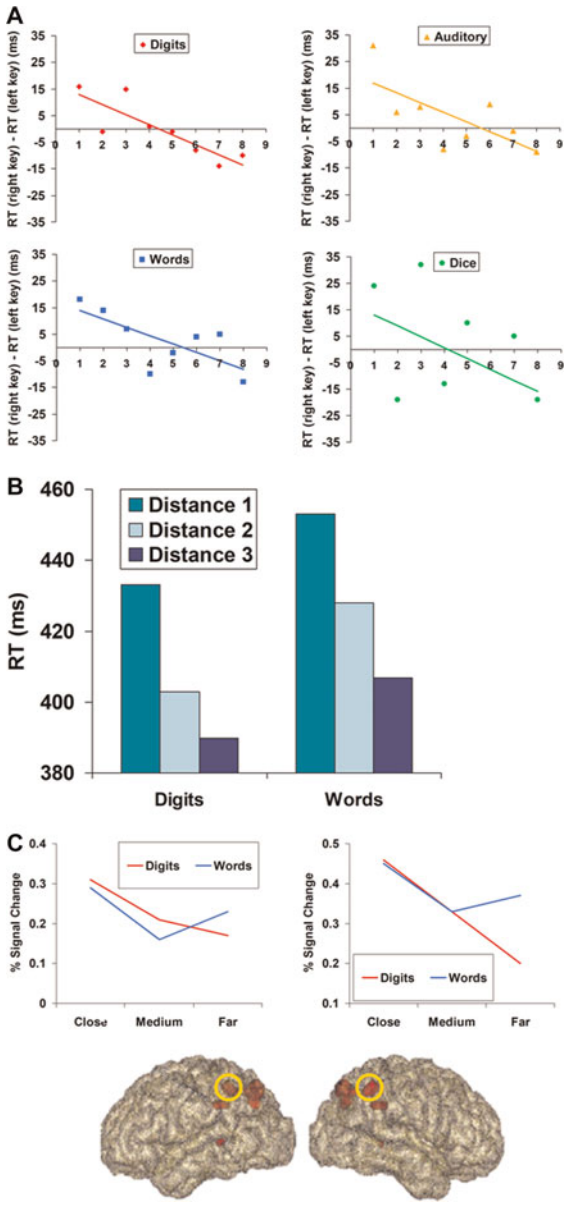


Figure 1. Effects that underlie the idea that numerical representation is abstract. (**A**) The SNARC effect for different notations (digits, words, dice) and modalities (visual, auditory). In this experiment the subjects were instructed to decide whether a numerical stimulus is odd or even (i.e., parity judgement) by pressing the right or the left response key (key assignment was counterbalanced within subjects). The slopes that were obtained are independent of format. (**B**) The Distance effect for digits and words shows the same function independent of notation. In this experiment subjects were asked to decide by a button press whether the displayed number (i.e., the numbers 1 to 9, excluding the number five) is numerically larger or smaller than the standard number five. (**C**) Brain activation in the IPS (in orange circles) is modulated in similar ways as a function of the numerical distance between the compared digits, independent of the notations that were used (i.e., words or digits). Left IPS appears on the left side, right IPS appears on the right side. In this experiment the subjects decided whether a visually presented number was larger or smaller than a fixed reference number (65) by pressing a button with their right or left hand according to instructions. Adapted from Nuerk et al. (2005), Pinel et al. (2001), and Schwarz and Ischebeck (2000) with permission. A color version of this figure is available online at www.journals.cambridge.org/bbs.

(e.g., digits, verbal numbers, numerosity, Mandarin numerals) (Campbell & Epp 2004; Dehaene 1996; Dehaene & Akhavein 1995; Droit-Volet et al. 2008; Ganor-Stern & Tzelgov 2008; Koechlin et al. 1999; Reynvoet & Ratinckx 2004) or modalities (i.e., visual or auditory) (Barth et al. 2003), but the implications of most of these results have either been ignored, or alternative explanations have been given that leave the idea of non-abstract representations unchallenged.

In addition to the fact that similar behavioural effects can be produced by different mechanisms (Cohen Kadosh et al. 2007a; Rumelhart & McClelland 1986), at the neuronal level, similar brain activations can stem from different neuronal populations that are co-localised within a single imaged voxel (volumetric pixels) and cannot be segregated with conventional neuroimaging techniques (Cohen Kadosh et al. 2007b; Grill-Spector et al. 2006b; Nieder 2004). In other words, in the parietal lobes each voxel that is activated is sampled during the functional magnetic resonance imaging (fMRI) experiment (with a spatial resolution of ~ 3 cubic mm) and contains about 1.25 million neurons (Pakkenberg & Gundersen 1997). Moreover, the neurons in this voxel can fire tens of impulses per second for different functions. However, different functions cannot be detected, as the fMRI signal – which indicates an increase in oxygenated blood bringing energy to active neurons – develops sluggishly, over several seconds. Therefore, observing similar activations at the voxel level for different notations (Pinel et al. 2001) or modalities (Eger et al. 2003), or alternatively, observing similar time courses in event-related potentials (ERP) experiments that lack spatial resolution (Dehaene 1996; Libertus et al. 2007), is not sufficient to indicate abstract representation. This theoretical point is gaining experimental support from single-cell neurophysiology in monkeys. It has been shown, for example, that neurons that are sensitive to numbers, are also sensitive to features that have little to do with magnitude information (Nieder et al. 2006; see also Calabrese 2007). Note that such a finding, although not speaking directly against the idea of abstract numerical representation, challenges the idea that numerical or magnitude representation is modular (Dehaene et al. 1998; McCloskey 1992). Indeed modular representation of any single class of stimulus features of the world does not have a good history. Suggestions that the monkey or human brain contained a colour centre (Lueck et al. 1989; Zeki 1980), a motion centre (Zeki 1974), or a word form area (Cohen et al. 2000; McCandliss et al. 2003) – all good cases for attributes of the external world that one might expect to have a single locus of representation – have been found wanting; and each of these attributes has been found either to be multiply represented for different task demands at almost every level of the visuocognitive system (cf. Orban et al. 1996; Otten & Rugg 2001; Watanabe et al. 1998) or the "centre" has been found to be not specific to the attribute (cf. Merigan 1996; Price & Devlin 2003; Xue & Poldrack 2007). A priori, number information – which is less constrained than simple object features such as colour, form, and motion, and upon which we perform explicit and implicit computations – would seem to be a poorer candidate for a canonical representation.

Numerical representation is also modulated by task and automaticity. Various definitions have been attributed to

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the concept of "automaticity" (e.g., Carr 1992; Hasher & Zacks 1979; Logan 1985; Posner 1978). In the current article, we adopt Tzelgov et al.'s (1996) definition (see also Barge 1992) that a process is automatic if it does not need monitoring to be executed. Most studies that support the idea of an abstract representation are based on subjects carrying out intentional processing of numerical information. However, numbers are also represented automatically (for a review, see Tzelgov & Ganor-Stern 2005). Automatic and intentional processing can lead to very different inferences about the underlying representation (Cohen Kadosh et al. 2008b; 2008g; Tzelgov & Ganor-Stern 2005), and brain activity (Cohen Kadosh et al. 2007a, Lewis & Miall 2003; Orban et al. 1996). Indeed, task-dependency is a fundamental feature of brain representation and has been reported at every level of every perceptual and cognitive domain, including time perception (Lewis & Miall 2003), magnitude processing (Cohen Kadosh et al. 2008c), face processing (Cohen Kadosh et al., in press), and visual processing (Orban et al. 1996). Mental representations can be probed when they are engaged by task demands or when their processing is automatic. The advantage of using automatic processing is that processing and behaviour are unaffected by task demands and intentional strategies (Cohen Kadosh et al. 2008b; 2008g; Tzelgov & Ganor-Stern 2005).

This might imply that specific task requirements may induce humans to generate different representations (e.g., shared representation for different notations). Clearly, humans *can* generate numerical representations according to task requirements (Bachtold et al. 1998; Fischer & Rottmann 2005; Gertner et al. 2009; Hung et al. 2008; Lindemann et al. 2008; Shaki & Fischer 2008; Shaki & Petrusic 2005). For example, Bachtold et al. (1998), in a numerical comparison task of the numbers 1 to 11 (excluding the number 6 which serves as the standard), found that subjects showed a normal SNARC effect when they conceived the numbers as distances on a ruler, which represents small numbers on the left and larger numbers on the right. Importantly, the SNARC effect was reversed (i.e., faster responses to small numbers with right-hand key responses than with left-hand key responses, and faster responses to large numbers with the left-hand key responses than with the right-hand key responses) when the subjects conceived the numbers as hours on a clock face, which presents small numbers on the right side, and large numbers on the left side. Thus, a limit to the abstract representation view we have to face is that observations consistent with shared representations may be true only for specific task conditions in any given experiment.

Clearly, then, the evidence that numbers are abstractly represented has several limitations: null results (Cohen Kadosh 2008a; Dehaene 1996; Schwarz & Ischebeck 2000; Shuman & Kanwisher 2004), technical limitations (Ansari 2008; Nieder 2004), and task specificity (Ansari 2007; Ansari et al. 2006a; Bachtold et al. 1998; Cohen Kadosh et al. 2008b; Göbel et al. 2004; Van Opstal et al. 2008a; Venkatraman et al. 2005; Wood et al. 2006a). In the next section, we provide evidence that directly challenges the idea that numbers are represented abstractly. The line of experiments we turn to next shows that non-abstract representations exist in a variety of tasks and cultures.

6. Two ≠ II and 2 does not equal two

Given the ubiquity and importance of numbers and the early stage in life at which we learn about them, it is not surprising that, like words, they are eventually overlearned and processed automatically. Automatic numerical processing is an important ability that exists not only in human adults (Cohen Kadosh 2008b; Cohen Kadosh & Henik 2006; Dormal et al. 2006; Fias et al. 2001a; Henik & Tzelgov 1982; Lammertyn et al. 2002; Pavese & Umiltà 1998; Schwarz & Heinze 1998; Schwarz & Ischebeck 2003; Tzelgov et al. 1992; Verguts & Van Opstal 2005), but also in children (Gebuis et al. 2009; Girelli et al. 2000; Mussolin & Noel 2007; Rubinsten et al. 2002; Szucs et al. 2007; Zhou et al. 2007), and animals (Washburn 1994). The automaticity of numerical information processing gives one the opportunity to explore numerical representation per se, independent of one's strategies (Cohen Kadosh et al. 2008g; Ganor-Stern & Tzelgov 2008; Tzelgov & Ganor-Stern 2005). Automaticity has been explored mainly by using conflict tasks, for example, the size congruity paradigm. Usually, in this paradigm subjects are presented with two digits on the computer screen (one digit in the left visual field, and one digit in the right visual field) and are required to compare the stimuli according to their physical size while ignoring their numerical value (e.g., 2 4), and to press the button that corresponds to the side of the physically larger stimulus (Cohen Kadosh 2008b; Cohen Kadosh & Henik 2006; Gebuis et al. 2009; Girelli et al. 2000; Henik & Tzelgov 1982; Mussolin & Noel 2007; Rubinsten & Henik 2005; 2006; Rubinsten et al. 2002; Schwarz & Heinze 1998; Schwarz & Ischebeck 2003; Szucs et al. 2007; Tzelgov et al. 1992; Verguts & Van Opstal 2005; Zhou et al. 2007). The stimuli can be incongruent (the physically larger digit is numerically smaller; e.g., 2 4), neutral (the stimuli differ only in the relevant dimension; e.g., 2 2), or congruent (the physically larger digit is also numerically larger; e.g., 2 4). A common finding is that incongruent trials, being slower to process than congruent trials (size-congruity effect), as reflected by slower RT, indicate that the numerical information is processed automatically. This paradigm has been employed in behavioural studies and has yielded an interaction between different notations and automatic processing of numerical information (Cohen Kadosh et al. 2008e; Ito & Hatta 2003). For example, Ito and Hatta (2003) found that when participants compared the physical size of Kana scripts – the equivalent of verbal numbers – numerical information was not processed automatically. Therefore, the irrelevant numerical information did not interfere with the relevant physical size judgement. In contrast, when the same participants compared digits or Kanji numbers (ideographic script), a size-congruity effect was observed, thus indicating that the numerical information was processed automatically, and interfered the relevant physical size judgement. Similar results were found and extended by another laboratory (Cohen Kadosh et al. 2008e).

A recent study used a simple comparison task in which subjects had to compare the numerical values of digits or verbal numbers while examining the effect of numerical information in trial $n - 1$ on processing of numerical information in trial n (i.e., sequential effect) (Cohen Kadosh

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2008a). Others conducted a similar analysis on a similar numerical task (Dehaene 1996; Schwarz & Ischebeck 2000) and similar stimuli (Dehaene 1996), and did not find an interaction between notation and the distance effect or differential effects of trial $n - 1$ on trial n as a function of notation. However, these studies used a long response-to-stimulus-interval (RSI) (>1,500 msec), which is likely to produce expectancy effects (Soetens 1998), whereas automatic processing occurs under short RSI conditions (e.g., ≤200 msec) (see Neely [1977] for a similar idea for priming tasks). By using a short RSI of 200 msec, and a large number of subjects and trials, three results emerged which support the idea that non-abstract representations of numbers exist: (1) an interaction between notation and numerical distance in reaction time; (2) an interaction between notation, notation repetition, and numerical distance in error rates; and (3) an interaction between notation and the distance between the numerical distance in trial $n - 1$ and trial n with reaction time as the dependent variable (Cohen Kadosh 2008a).

Dehaene and Akhavein (1995) used a same-different task, in which participants were asked to decide via a button press whether two members of a pair of stimuli, which are presented simultaneously, were the same or different. The notations were digit-digit (e.g., 2-2, 2-8), verbal number-verbal number (e.g., TWO-TWO, TWO-EIGHT), or a mixed notation (e.g., verbal number-digit; TWO-2, TWO-8). When the subjects compared the similarity of the numbers according to their numerical values, a distance effect independent of notation was observed. In contrast, in physical matching, when the participants compared the numbers according to their perceptual similarity, an interaction between notation and the distance effect was observed with a flat and not significant distance effect for mixed notation. Although the latter finding indicates that numerical representation is non-abstract, because numerical processing should be observed independent of the input (i.e., mixed notation vs. pure notation), Dehaene and Akhavein (1995) argued that numbers, whether digits or verbal, converge towards a common semantic representation.

In a recent study, Ganor-Stern and Tzelgov (2008) conducted two experiments: one with a same-different task and another with the size congruity paradigm. The same-different experiment was similar to Dehaene and Akhavein's (1995) study but with Indian numbers (a different notation for numbers that is used mostly in Arabic-speaking countries) instead of verbal numbers. In the physical comparison task they were not able to replicate the distance effect for digits, Indian numbers, or mixed notation. However, they argued that numbers were still processed automatically by finding what they called the "value interference effect," that is, processing the numbers' numerical value impaired participants' "different" responses to different-notation pairs with the same numerical values (e.g., 8 in digit notation vs. 8 in Indian notation) compared with those with different numerical values (e.g., 8 in digit notation vs. 2 in Indian notation). However, this effect does not indicate semantic processing and it can be attributed to asemantic transcoding (e.g., due to phonological representation). In this case, the digit 8 and the Indian number 8 were recognized as representing the same numbers, even though the numerical representation was not accessed (see Dehaene & Akhavein 1995, for a discussion on this scenario). Indeed, the lack of distance effect in Ganor-Stern and Tzelgov's (2008) experiment supports the idea that numerical information did not reach the level of the semantic representation. In another experiment, Ganor-Stern and Tzelgov found that digits, Indian numbers, and mixed-notation (digit and Indian numbers) caused interference to a physical size judgment, as reflected by the size-congruity effect. Again, they argued that this effect indicates abstract representation. However, one should note that the level of the interference interacted with notation, as well as with the numerical distance, thus replicating the findings by Ito and Hatta (2003) and Cohen Kadosh et al. (2008e). This result can be explained not as a result of abstract representation, but simply an interference during response selection, as was shown in several ERP and fMRI studies (Cohen Kadosh et al. 2007c; 2008d; Szűcs & Soltész 2007; Szűcs et al. 2007). Moreover, in another experiment, when subjects were asked to compare pairs of numbers for their numerical value, Ganor-Stern and Tzelgov found that the distance effect was modulated as a function of notation (i.e., interaction between notation and distance effect).

Together, these interactions provide results which cannot be explained by assuming an abstract representation – therefore challenging the central idea that numbers are processed in an abstract fashion, as was strongly suggested by the different architectures for numerical cognition (e.g., the abstract modular model [McCloskey 1992] and the triple-code model [Dehaene 1992] discussed earlier). Nevertheless, Ganor-Stern and Tzelgov (2008, p. 430) reached the conclusion that: "different notations are automatically translated into a common representation of magnitude, in line with M. McCloskey's (1992) abstract representation model." However, as we have shown, examination of the details of their results does not allow one to conclude that numerical representation is abstract; rather, it seems to strongly support our view that numerical representation is not abstract.

In another study (Droit-Volet et al. 2008) 5-year-olds, 8-year-olds, and adults participated in a number bisection task in which numbers were presented sequentially to one group of participants or simultaneously to another group of participants. In this task, the subjects are trained to discriminate a "few" standard (e.g., 8 dots) from a "many" standard (e.g., 20 dots). They were then presented with comparison stimuli that contain intermediate values (e.g., 12 dots) or values equal to the standard, while being asked to decide if the comparison stimuli is more similar to the few or many standard. They found that the mode of presentation yielded different Weber-ratios (which indicate the sensitivity to discriminate two numbers). Namely, the Weber-ratio was larger during sequential presentation of numerical quantity compared to simultaneous presentation, and this difference was highly significant for adults and 8-year-old participants, and showed only a trend in the case of 5-year-old children. Importantly, this study, as in the study by Cohen Kadosh (2008a), used a large number of participants (more than 60 participants in each group), and thus increased the statistical power and sensitivity to evidence of non-abstract representation.

Other evidence which challenges the existence of abstract numerical representation and supports the

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existence of non-abstract representations comes from a recent study by Dehaene and colleagues (Dehaene et al. 2008). In their study, subjects from the Mundurucu tribe, an indigenous Amazonian group with a reduced numerical lexicon and little or no formal education, had to indicate the location of a given number (e.g., 6 dots) on a line segment with 1 dot at left and 10 dots at right. The number to be mapped appeared in a random order and in various forms (sets of dots, sequences of tones, spoken Mundurucu words, or spoken Portuguese words). For each number, adults and children pointed to a screen location. The responses for both children and adults were best fitted with a logarithmic curve (i.e., the larger the numbers were, the more closely they were mapped), a response that in the western culture is usually characteristic of young children (Siegler & Booth 2004). In contrast, the responses of adults who have been through a longer educational period were best fitted with a linear curve. Importantly, performance varied significantly with number notation within the more educated group. Responses for Portuguese numerals were best characterized by a linear function, but logarithmic for Mundurucu numerals and dot patterns from 1 to 10. These findings cannot be explained by an abstract representation, as different verbal numbers such as the Portuguese word QUATRO and the Mundurucu word EBADIPDIP donate the same number (FOUR) and should have led to similar mapping of the numbers independent of their notations.

Some evidence for non-abstract representations comes from replications of classic effects. For example, a recent study examined the effect of different notations on the SNARC effect (Hung et al. 2008). In this study, the participants were asked to make a parity judgement, similar to the study by Nuerk et al. (2005) that we described earlier (sect. 4, and Fig. 1a). While the numerical information in the study by Nuerk et al. (2005) could appear as digits, German words, auditory German words, or as on a dice, the numerical information in Hung et al. (2008) appeared in three different notations: digits, which appeared horizontally in text, Chinese numerical words in the simple form (e.g., 一), and in the complex form (e.g., 壹), which are presented in vertical text. Hung et al. did find that the SNARC was affected by the numerical notation, as indicated by the interaction between the magnitude category and the responding hand (i.e., the SNARC effect) and notation. This interaction was due to the SNARC effect only for digits. Inspired by previous studies that found the SNARC effect also with vertically aligned manual responses (faster responses to small numbers with bottom-hand key responses than with top-hand key responses, and faster responses to large numbers with the top-hand key than with the bottom-hand key) (Gevers et al. 2006a; Ito & Hatta 2004; Schwarz & Keus 2004), they examined the effect of notation on this vertical SNARC effect. They found a consistent SNARC for the Chinese verbal numbers, but not for the other notations. The results might indicate, as Hung et al. suggested, that the representation of numbers in space is influenced, if not determined, by the dominant reading/writing experience. It is an open question why Nuerk et al. (2005) obtained a null result for the interaction between the SNARC effect and notation. Different subjects, cultures, and stimuli, might contribute to the discrepancy between the studies. Nevertheless, the current study shows that different notations lead to different mapping of numbers in space. As mapping of numbers in space was shown to take place during the numerical representation (Mapelli et al. 2003; Zorzi et al. 2002), or even later, during the response selection (Gevers et al. 2006b), this result indicates that different notations do not converge into an abstract, single-representation, at least at the level of the numerical representation, and maybe even later.

Koechlin et al. (1999) conducted several experiments on priming and subliminal priming. In these experiments the subjects were asked to compare a stimulus (e.g., the number 4) to the number 5, which served as a standard. The numbers could appear as digits, verbal numbers, or numerosity. Although most of the findings by the authors were compatible with the abstract representation view (i.e., they did not find an interaction between distance and notation), the authors also obtained some results that are more in line with the non-abstract representation view. For example, in one experiment they used verbal numbers and digits. Although they did not find an interaction between notation and distance under regular priming, they obtained this interaction under subliminal priming (which might reduce subjective expectancy/strategies). In another experiment, they used numbers in digits or numerosity notations. They found an interaction between notation and quantity priming (reduction in RT as the numerical distance between the prime and target reduced), in both regular and subliminal priming. These results indicate that there are different representations of digits, verbal numbers, and numerosity. Subsequently, Koechlin et al. proposed the existence of separate notation-specific representations of quantity that converge at a post-representational stage of processing. It is important to note that they assumed that these distinct representations are revealed only under a demanding temporal condition (e.g., subliminal priming in which the prime is presented for as little as 66 msec). Nevertheless, this position has been ignored by most researchers in the field in favour of the abstract representation viewpoint.

Another effect which shows that numerical representation is not abstract is the compatibility effect (Nuerk et al. 2001; 2004a; 2004b; Wood et al. 2006b). The compatibility effect indicates that when people are comparing two two-digit numbers they are faster to compare the numbers if both the units and decades of a given number are systematically smaller or larger. For example people will be faster to compare the number 42 vs. 57 ($4 < 5$, and $2 < 7$) than 47 vs. 62 ($4 < 6$, but $7 > 2$). This effect seems to be independent of the distance effect (in both examples the distance effect is equal) (Nuerk et al. 2001; 2004b) or response selection (Nuerk et al. 2004a). This effect indicates that the numerical representation is not unitary, even within a single value (Dehaene et al. 1990), but might incorporate additional representations for tens and units. Importantly, the compatibility effect seems to be modulated as a function of notation. That is, the compatibility effect is smaller for verbal numbers than for digits (Nuerk et al. 2002).

Further support for the non-abstract view comes from a recent developmental study. Holloway and Ansari (2009) collected the reading and mathematical achievements of

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children at the ages of 6 and 8 years. The mathematical examination required the participants to answer as many single-digit addition, subtraction, and multiplication problems as possible within a 3-minute period. The reading skills were tested using a letter–word identification in which the participants needed to correctly read real words aloud to the experimenter, and word attack subtests, which required them to correctly pronounce pseudowords. Holloway and Ansari correlated these scores with the distance effect that was observed when these children compared numbers in digits (symbolic) or squares (non-symbolic) notations. The abstract representation would predict that the distance effect independent of notation might correlate with mathematical achievement. In contrast, the distance effect was only correlated with mathematical achievement (but not reading achievements) when the numerical notation was in digit form. In contrast, the distance effect when numbers appeared as squares did not predict mathematical achievements. Moreover, they also found an interaction between distance and notation, and a lack of correlation between the distance effect for digits and squares. These results clearly suggest that different developmental trajectories underlie the representation of symbolic and non-symbolic numerical magnitude. However, Holloway and Ansari interpreted these findings as resulting from a better mapping between digits and numerical magnitudes in children with better mathematical achievement, despite the fact that a better mapping of digits to abstract representation can explain overall faster RTs in children with better mathematical achievement, but cannot explain the differences in the distance effect, as the symbolic distance effect occurs at the level of the representation (Dehaene 1996; Schwarz & Ischebeck 2000) or even later, during response selection (Cohen Kadosh et al. 2008b; Link 1990; Van Opstal et al. 2008a; Verguts & Fias 2004), but certainly not earlier.

Other differences between different numerical notations have been found when stimuli have been processed automatically. However, in these cases the explanations provided considered only what was consistent with the abstract view. For example, Fias (2001) used the SNARC effect to examine the processing of verbal numbers. A SNARC effect was observed when the participants were asked to make a parity judgement, but was not found when verbal numbers were processed automatically, that is, when the participants were asked to monitor the occurrence of certain phonemes of verbal numbers (i.e., whether there was an /e/ sound in the name of the written verbal number). Notably, in a previous study, the SNARC effect was observed for both parity and phoneme monitoring tasks with digits (Fias et al. 1996). These findings suggest that under unintentional processing, the spatial representation of the two notations might differ. However, Fias (2001) suggested that this difference between digits and verbal numbers was a result of inhibition of the semantic route by the non-semantic route only in the case of verbal numbers. Other studies also found a dissociation between digits and verbal numbers; however, these studies used naming tasks (Fias et al. 2001b; Ischebeck 2003). Compared to manual tasks, naming tasks are prone to include verbal/phonological processes, because words are the preferred output format for naming (Dehaene 1992). However, this explanation cannot account for the differences between different numerical notations in the studies that we described earlier, as they all required a manual response (Cohen Kadosh 2008a; Dehaene & Akhavein 1995; Dehaene et al. 2008; Droit-Volet et al. 2008; Ganor-Stern & Tzelgov 2008; Ito & Hatta 2003). Thus, it might be that the differences between the notations reflect, at least partly, non-abstract representations, rather than solely preferred output format for naming (Dehaene 1992).

Neuroimaging studies that have employed the size congruity paradigm using a single notation (Cohen Kadosh et al. 2007c; Kaufmann et al. 2005; Pinel et al. 2004; Tang et al. 2006a) found activity associated with interference between digits and physical size in the IPS (i.e., larger BOLD signal change for an incongruent condition vs. congruent condition). However, when different notations are used (Ansari et al. 2006b; Shuman & Kanwisher 2004) these interference effects are not seen in the IPS, thus supporting the idea of non-abstract representation.

Numbers are apprehended automatically and even passively viewing them can activate a sense of magnitude, and therefore modulate neural activation in the IPS (Cantlon et al. 2006; Piazza et al. 2004). This is an important issue because at least one previous study has shown that the activation in the IPS during intentional numerical processing can be due to response selection rather than numerical representation (Göbel et al. 2004). This methodological confound may therefore explain IPS activation that is attributed to numerical processing (Eger et al. 2003; Naccache & Dehaene 2001a; Pinel et al. 2001) when similar response selection demands are associated with different types of representation, a proposition that is in line with recent studies (Cohen Kadosh et al. 2008b; Van Opstal et al. 2008a). Eger and colleagues (Eger et al. 2003), for example, used a numerical target detection task to avoid using direct magnitude judgements. In this task, the nine subjects were presented with numbers between 1 and 9 and required to detect, via a button press, the appearance of a target number (e.g., 7). Numbers have been found to activate the IPS independent of modality (visual or auditory presentation). However, this task required the subjects to:

1. Process the numbers intentionally.
2. Look for a target number independent of modality.

Given that the numerical representation is flexible and biased by task requirements (e.g., Fischer & Rottmann 2005; Gertner et al. 2009; Shaki & Petrusic 2005) this may lead the subjects to create a modality-independent *response* set.

3. Prepare a similar response selection for each type of representation: The closer the number is to the target the more likely it will be that the activity associated with response selection is similar across stimulus types (i.e., pressing the button when detecting the target). For example, if the target number is 7 ("SEVEN"), 6 ("SIX") is numerically closer to 7 than 1 ("ONE"). This idea has been confirmed by behavioural results (Cohen Kadosh et al. 2008b; Van Opstal et al. 2008a).

To examine whether numerical representation is abstract and independent of task requirements, two recent studies (Cohen Kadosh et al. 2007b; Piazza et al. 2007) employed passive viewing in a modified adaptation paradigm (Grill-Spector et al. 2006a; Sawamura et al.

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2006). Using this paradigm, the repetition of the same stimulus reduces the responsiveness of single neurons in monkeys (Sawamura et al. 2006) and the BOLD signal in humans (Grill-Spector et al. 2006a). In humans, BOLD signal adaptation occurs when the stimulus changes indicate that the neurons are not affected by the stimulus-specific adapting attribute. In contrast, BOLD signal recovery from the state of adaptation implies that different neuronal populations are activated and that these neurons are therefore differentially sensitive to some property of the adaptation and test stimuli. Recently, this paradigm has become popular in fMRI research, particularly because of the claim that it provides improved spatial resolution by revealing sub-voxel effects (Grill-Spector et al. 2006a). Therefore, the adaptation paradigm can be used to address some of the limitations discussed earlier, such as spatial resolution, subjects' strategies, and response selection. In the study by Piazza and colleagues (Piazza et al. 2007), for example, subjects passively viewed dot arrays or digits that varied in numerical value; a quantity presented to induce signal adaptation was followed by a deviation in the quantity to result in signal recovery. The abstract hypothesis suggests that similar adaptation and recovery should occur, irrespective of which combinations of dot arrays and digits were used at the adaptation and test phases. The logic behind this suggestion is that both notations denote the same numerical quantity, and therefore the same neuronal correlate should be sensitive to the numerical quantity, irrespective of its format (Dehaene et al. 1998; 2003). The results, however, challenged the abstract representation: that is, there was an interaction between notation and recovery in the left and right parietal lobes. Moreover, the abstract representation posits that the recovery of the BOLD signal following the deviant stimuli should be of the same magnitude, again, irrespective of notation. That is, greater recovery should follow large numerical deviation (e.g., the number 50 after constant presentation of quantities between 17 and 19) in comparison to small numerical deviation (e.g., the number 20 after constant presentation of quantities between 17 and 19), and the magnitude of the recovery should not interact with notation. This again was clearly not the case; the left IPS, showed an interaction between notation and recovery that was modulated as a function of numerical distance. Although the authors focused more on the similarity observed in the right IPS between the notations, as indicated by the failure to find a significant interaction between notation, recovery, and numerical distance, the interaction between notation and recovery in both left and right IPS, and particularly the interaction between notation, recovery, and numerical distance in the left IPS (Fig. 2a), lend themselves to an explanation in terms of non-abstract representation.

Cohen Kadosh and colleagues (Cohen Kadosh et al. 2007b) presented digits and verbal numbers in pairs. The pair could have an identical quantity (e.g., 8/eight after 8/eight), or a different quantity (e.g., 8/eight after 4/four). Adaptation was identified as the difference in the BOLD signal between pairs that did or did not differ in quantity. The results again indicated a deviation from abstract representation. Namely, the right IPS, but not the left IPS, showed an interaction between adaptation and notation. In

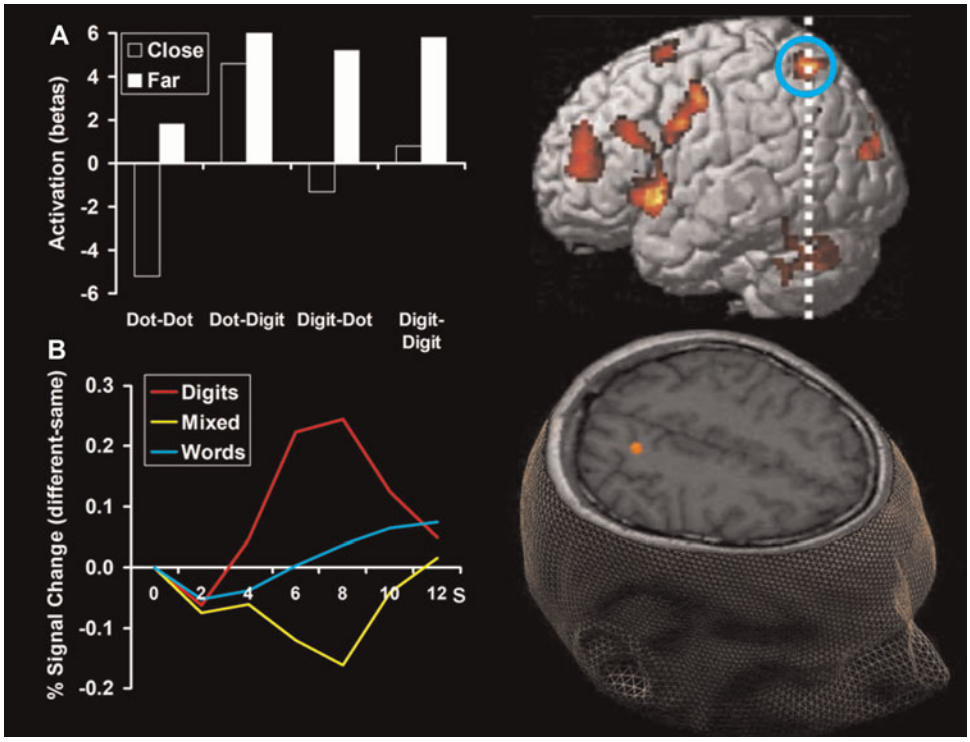


Figure 2. Evidence of non-abstract representations from recent neuroimaging studies. (**A**) From the left, the recovery effect following the adaptation period for dot arrays and digits due to numerical deviations (Far, Close) was modulated by notation in the left IPS (turquoise circle). (**B**) The right IPS shows an adaptation effect (different quantity minus same quantity) for digits, but not for words or mixed notation. (Adapted from Cohen Kadosh et al. [2007b] and Piazza et al. [2007] with permission.) A color version of this figure is available online at: www.journals.cambridge.org/bbs.

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particular, the adaptation in the right IPS appeared only when a digit preceded a digit (Fig. 2b). The results again challenge the idea that numbers are represented in an abstract fashion, in this case, in the right IPS, and are best explained in terms of non-abstract representation.

Thus, two studies, including one that purports to support abstract representation, reveal notation-dependent effects in the two key areas – the right and left IPS – associated with different numerical representations.

One might suggest that the lack of interaction between notation and adaptation in the left IPS in Cohen Kadosh et al.'s (2007b) study indicates the existence of an abstract representation. We examined the involvement of the left IPS in abstract representation by using a different technique, transcranial magnetic stimulation (TMS), together with an adaptation paradigm. This innovative combination of TMS and adaptation (termed TMSA) significantly increases the functional resolution and allows one to differentially stimulate distinct but spatially overlapping neural populations within a stimulated region (Silvanto & Muggleton 2008a; Silvanto et al. 2007). The paradigm is based on findings that the effects of TMS are determined by the initial neural activation state, with attributes encoded by the less active/excitable neural populations within the stimulated region being more susceptible to the effects of TMS. Thus, by using adaptation to manipulate neural activation states prior to the application of TMS, one can control which neural populations are stimulated by TMS (for reviews see Silvanto & Muggleton 2008b; Silvanto et al. 2008). In our experiment the subjects were adapted to the digit 7, which repeatedly appeared on the screen for 45 seconds in different locations and fonts. Following this adaptation period, the subjects had to decide in a same-different task whether two numbers, digits, or verbal numbers on the screen are perceptually the same or different, while we stimulated the IPS with TMS during the period of 180, 280, and 380 msec post-stimulus presentation – a timing during which numerical representation processes are believed to take place (Cohen Kadosh et al. 2007c; Dehaene 1996; Libertus et al. 2007; Szucs et al. 2007; Turconi et al. 2004). According to the abstract representation view, the participants' decision time would be affected by the adapted number 7, independent of the numerical notation. In contrast, if separate representations for digits and verbal numbers exist, as the non-abstract representation view predicts, one should expect to find that only the representation for digits was affected. The latter hypothesis was borne out. Only digits were affected by TMS to the left IPS, while words were not affected. Moreover, the TMS effect was most effective when the digit 7 appeared, and was attenuated as numerical proximity decreased. This was not the case for verbal numbers (Fig. 3). In a second experiment, the subjects were adapted to verbal numbers rather than digits. The results were exactly the opposite from the previous experiment, thus completing a double dissociation; TMS to the left IPS was most effective when the adapted verbal number appeared, and was attenuated as numerical proximity decreased. This experiment shows that non-abstract representations for digit and verbal numbers exist also in the left IPS (Cohen Kadosh et al., submitted b). These apparent differences between the neuroimaging findings and the current TMS results are most likely to be rooted in the fact that TMS and fMRI yield different measures of cause and correlation, respectively (Walsh & Pascual-Leone 2003).

7. Multiple representations of number

The fMRA findings in Piazza et al. (2007) and Cohen Kadosh et al. (2007b) and the TMSA results illustrate the idea that improved spatial resolution and automatic processing (or controlling for task-related responses) can uncover non-abstract representations that are otherwise masked. Notably, these studies used different notations, different ranges of numbers, different designs, and different techniques: the generalizability of these findings is therefore likely to be high. Differences in the results between these studies are also apparent. The results in Piazza et al. (2007) indicate that numerical representation for dots and digits is non-abstract in the left IPS, as illustrated by the interaction between notation and recovery (which was also significant for the right IPS) and notation, recovery, and numerical distance. In contrast, the study by Cohen Kadosh et al. (2007b) points towards the opposite conclusion, that is, that numbers in verbal number and digit notations are represented non-abstractly in the right IPS. However, the TMSA results showed that in the left IPS, too, numbers in verbal number and digit notations are non-abstractly represented. It seems clear, then, that non-abstract representation may be a feature of either IPS, and across different notations.

However, the parietal lobes in the fMRI studies also showed some pattern that at first sight supports the existence of abstract representation. There are four possibilities for this pattern:

1. Non-abstract and abstract representations coexist.

2. While an interaction between notations is a strong indication of the existence of non-abstract representation, the lack of such interaction does not necessarily indicate the existence of abstract representation, because it is based on an absence of evidence.

3. Piazza et al. (2007) did control for task-related responses, but explicitly asked the subjects to pay attention to the quantity conveyed by the stimuli, and they were informed about the different formats and their approximate values. Moreover, immediately prior to the scanning session, subjects were shown approximately four exemplars of each numerosity (17:20 and 47:50 dots) and informed about their approximate range (~20 and ~50, respectively) in order to calibrate them to the respective value (Izard & Dehaene 2008). Therefore, one cannot be sure if at least some of the subjects still processed the numbers intentionally (e.g., noting themselves that the number 49 was changed to 18 dots).

4. As originally pointed out by Piazza and colleagues (Piazza et al. 2007; for similar view, see also Tudusciuc & Nieder 2007), to explain the cross-adaptation that they observed, the apparent support for abstract representation within the parietal region might be due to non-abstract numerical representations that are characterised by separate but highly interconnected subassemblies of neurons. Therefore, when notations are mixed, activation of one given population (e.g., digits) would quickly spread to the other population (e.g., dots), thus leading to cross-notation adaptation in the absence of real abstract representation. This idea gains support from findings in the primate brain. For

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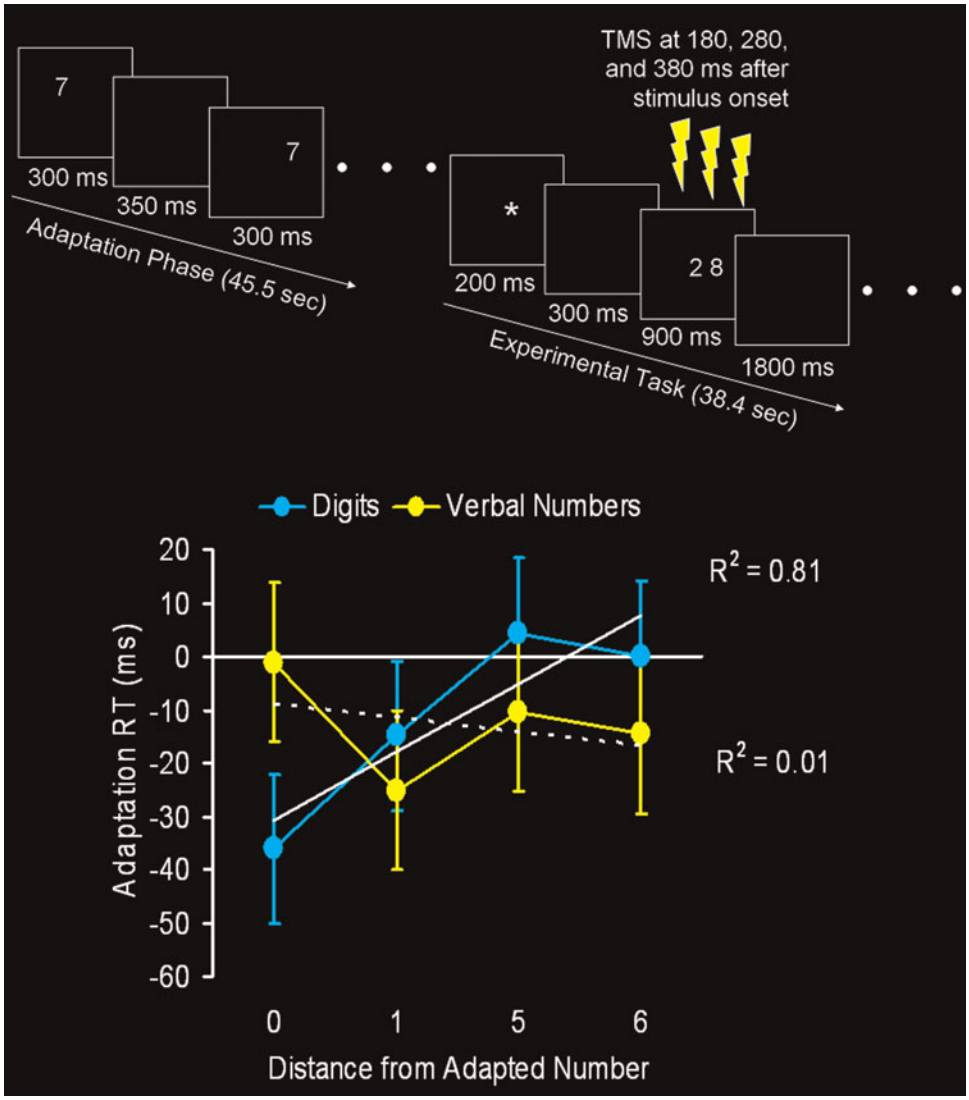


Figure 3. Non-abstract representations for digits and verbal numbers in the left IPS. In this TMS-adaptation experiment, the subjects were adapted to the digit 7. Top panel: Following this adaptation period the subjects had to decide whether a pair of numbers is perceptually same or different, while TMS was delivered to their IPS. Bottom panel: Adaptation was appreciated by the subtraction of the RT from a baseline condition, in which during the adaptation period the symbol # was presented instead of the digit 7 (i.e., no adaptation for numbers). TMS modulated only digits but not verbal numbers, as indicated by the interaction between notation and distance from the adapted number. This effect was maximal for the adapted digit, and reduced as the numerical distance from the adapted number increased. The straight white line shows the linear trend for the digits (which was significant), while the dotted white line shows the trend for the verbal numbers (which was not significant). A color version of this figure is available online at www.journals.cambridge.org/bbs.

example, based on fMRI studies in humans it was believed that both covert and overt shift of attention are subserved by the same mechanism in the frontal eye fields (FEF) (Corbetta et al. 1998). However, single-neuron recordings in monkeys, which provide better spatial and temporal resolutions, demonstrated that covert and overt shift of attention in the FEF are associated with different neural populations (Sato & Schall 2003), and that these dissociable populations are functionally interconnected (Schafer & Moore 2007).

8. Resolving the resolution problem

Single-cell neurophysiology offers better temporal and spatial resolution than human neuroimaging, and several recent studies have reported neuronal responses to quantity in the monkey brain (Nieder & Miller 2003; Roitman et al. 2007), which resemble the predictions of numerical-related behavioural effects and computational models (Verguts & Fias 2004).

Neuronal populations coding for numbers are highly distributed in the IPS, and also highly overlapping with representations of other magnitudes (for a neuroimaging meta-analysis, see Cohen Kadosh et al. 2008f), therefore making it difficult to disentangle numerical representation from other magnitudes. However, a recent single-cell neurophysiology study provided evidence for the existence of neurons that are specialized for different magnitudes (Tudusciuc & Nieder 2007).

Another study that examined whether numerical representation depends on the format of presentation

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demonstrated that in the macaque parietal cortex responses to the same quantity are initially format-dependent (Nieder et al. 2006); different neuronal populations discharge to sequential presentation, while others discharge to simultaneous presentation of numerosity. At a later stage during the delay period, these format-dependencies converge to a shared representation of quantity in the parietal cortex. This shared representation may be due to recurrent processing in the prefrontal cortex, which was not examined in the current study, but it showed longer latency and greater activity during the memory-delay period compared to the parietal cortex in a previous study (Nieder & Miller 2004). This suggests that the parietal lobe is equipped with primary non-abstract representations that are later transformed into a shared representation, possibly due to the intentional task requirement. Recently, Diester and Nieder (2007) showed that the neuronal populations for dots and digits in the parietal cortex of monkeys are notation-dependent. After training the monkeys to discriminate dot quantities, the monkeys were trained to associate digits with their corresponding dots (e.g., the digit 2 with two dots). Similar to humans, the behavioural results for digits and dots showed a similar function. However, Diester and Nieder (2007) found that whereas many neurons in the prefrontal cortex (PFC) were activated by digits, dots, or by both digits and dots, neurons in the parietal cortex were activated primarily for *either* digits or dots (Fig. 4). Further training may lead to different representations (e.g., further specialisation, or alternatively a convergence towards a shared representation) and awaits further exploration. Of course, this result cannot give us 100% confidence that the basic representation of numbers in the *human* parietal lobes is non-abstract, because of the comparative question. However, it shows that even after months of training and although digits were explicitly associated with their corresponding dots, it is possible for neurons in the parietal lobes to be non-abstract. This result, together with the behavioural and neuroimaging data in humans (sect. 6), supports the idea that non-abstract representation is the basic representation in the parietal lobes.

9. Prefrontal cortex and number: Operations not representations

We have confined our discussion so far to the parietal lobes, while not discussing the PFC. Some might argue that the PFC in the Diester and Nieder (2007) study showed some pattern that might be compatible with the idea of abstract representation (although one should note that the majority of the neurons there showed activation that is in

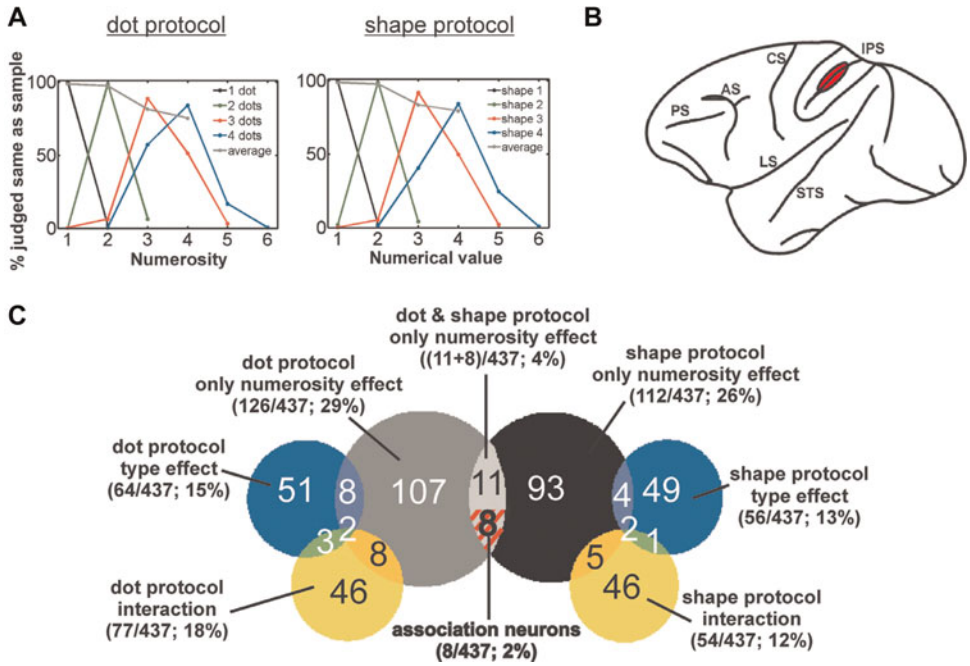


Figure 4. Non-abstract numerical representations in the monkey's IPS. Two rhesus monkeys (*Macaca mulatta*) were trained initially in a delayed match-to-sample protocol to discriminate small numbers of dots (between 1 and 4). Later, over several months they learned to associate visual shapes (the digits 1, 2, 3, and 4) with corresponding numerosities. Finally, both notations appeared in a randomised manner within an experimental session. (**A**) Behavioural performance for Monkey #1 for dots and shapes. The curves show how often the monkeys judged the first test and sample to be equal. The performance to discriminate dots or shapes between 1 and 4 was quite high and comparable. (**B**) Lateral view of a monkey brain. The red circle represents the location of recording sites in the parietal lobe. (**C**) Venn diagram summarising the results in the IPS. Numbers correspond to the numbers of neurons selective for each class. Association neurons indicate neurons that have similar tuning functions for the numerical values in both protocols; Numerosity effect corresponds to neurons that were selective for a particular number; Type effect indicates neurons that were modulated by non-numerical visuospatial properties (e.g., physical size, font). It appears that most of the neurons in the IPS were non-abstract, as they showed selectivity for dots *or* shape (digits). In contrast, the amount of "abstract" neurons (coding both dots and shapes) was negligible. AS = arcuate sulcus; CS = central sulcus; PS = principal sulcus; STS = superior temporal sulcus; LS = lateral sulcus. (Adapted from Diester and Nieder [2007]. A color version of this figure is available online at www.journals.cambridge.org/bbs.

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line with non-abstract representation). In terms of number research, the PFC has received less attention than the parietal cortex, but it is increasingly being seen as important in the field of numerical cognition, which starts mainly from the observation of numerons (neurons which are number-sensitive) in the PFC by Nieder and colleagues (Nieder et al. 2002). There is no doubt that the PFC is involved in numerical processing (for a recent review, see Ansari 2008). However, we argue that the PFC is not involved in numerical representation, at least not in humans. The PFC is important for some numerical *operations*, but not representations (Duncan 2001; Revkin et al. 2008).

The cognitive system is replete with such dissociations of cognitive operations and sensory representations – the hippocampus, while important for reconstructing memories, does not contain the representations of the objects in those memories; the PFC is involved in sequencing behaviours, while not containing the representations of each action in a sequence; the cerebellum is important for skilled use of fingers and motor coordination, but its role may be to support cognitive functions which are implemented by other brain areas (Glickstein 2007; Rosenbaum et al. 2001). There are several other reasons for our emphasis on the parietal cortex.

First, in human adults, only the IPS shows number-specific activation. This does not mean necessarily that this area is solely active in response to the given process. Posner (2003) encapsulates this view in another context in which he refers to activations observed in the same brain area under different task conditions:

> Although it is not always easy to distinguish between a brain area being specific for a domain or performing a computation that is of particular importance for some domains, either can underlie a form of modularity …. Thus these areas and many others that have been described are modules in the sense that they perform specific mental operations … sometimes the operations are within a single domain, but sometimes they are more general. (Posner 2003, p. 450)

In line with this idea, parts of the IPS show number-specific activation (Cohen Kadosh et al. 2005; 2008c). This was not found in the case of the PFC, which shows specificity for non-numerical magnitudes rather than numbers (Cohen Kadosh et al. 2005) or joint activation for numbers and other magnitudes (Cohen Kadosh et al. 2008c).

Second, the activation in the PFC may reflect other factors than representation including training, working memory, strategy application (Gilbert & Burgess 2008), or changes in response strategy (although some of them are also modulated by the parietal cortex, as was described in sect. 5). For example, neurons in the PFC might respond to dots and digits because there is a similar response strategy for the digit 1 and the dot 1 when comparing them to other stimuli presented. Similarly, Tudusciuc and Nieder (2007) have suggested that the PFC activation might relate to other functions of the PFC (e.g., cognitive control, working memory) that operates on parietal lobe functions (Miller & Cohen 2001).

Third, neuropsychological studies have found that neurological damage to the PFC leads to deficits in estimation, not because of representation impairment, but because of impairment at the level of translation from semantic representation to output (Revkin et al. 2008).

Fourth, there seems to be a shift from relying on the PFC during numerical processing to the IPS, as age increases (Ansari & Dhital 2006; Ansari et al. 2005; Cantlon et al. 2006; Kaufmann et al. 2006). This decrease in the reliance on prefrontal regions, and the increase in posterior specialized neuronal circuits, might relate to increased reliability of processes of cognitive control, attention, and working memory with age (Ansari 2008), or might indicate the developmental transition into a stage in which numerical representation becomes more automatic, and therefore involves less PFC resources.

Fifth, in contrast to many studies that consistently found that parietal damage leads to acalculia and basic numerical processing deficits (Ashkenazi et al. 2008; Dehaene & Cohen 1997; Delazer & Benke 1997; Delazer et al. 2006; Lemer et al. 2003; Takayama et al. 1994; Van Harskamp & Cipolotti 2001; Van Harskamp et al. 2002; Vuilleumier et al. 2004), there is, at least to our knowledge, a lack of consistent evidence of acalculia resulting from frontal damage. In this respect, we do not refer to secondary acalculia – numerical difficulties due to non-numerical origin, such as working memory problems (Doricchi et al. 2005) – but to a primary acalculia, which is rooted at the level of the numerical representation.

Sixth, in monkeys, numerical information is first coded in the parietal lobes, and only later in the prefrontal cortex. This temporal lag is in line with our suggestion that the PFC is involved in numerically-related processes, which might be post-representational (Nieder & Miller 2004).

Still, in humans, it is possible that the PFC is involved in numerical representation, rather than operation, during early developmental stages. This idea is gaining support from several neuroimaging studies that found PFC activation in children and infants during numerical tasks (Ansari & Dhital 2006; Cantlon et al. 2006; Izard et al. 2008; Kaufmann et al. 2006). The idea that children activate brain regions that are outside the typical areas activated in adulthood is not unique to the field of numerical cognition, and is observed in other fields. For example, children represent faces in additional cortical areas to the occipitotemporal network: occipital face area (Pitcher et al. 2007), fusiform face area (Kanwisher et al. 1997), and the superior temporal sulcus that are consistently found in adults (Haxby et al. 2000), including the left and right PFC (Gathers et al. 2004; Passarotti et al. 2003). (For a review, see Johnson et al. 2009.)

One of the reviewers rightly pointed out that in the recent fMRI study by Piazza et al. (2007), which we discussed in section 6, PFC activation was observed as a function of numerical processing, although the (adult) subjects passively processed the quantity. However, as was described in section 7, in this study Piazza and colleagues draw the attention of the subjects to the different numerical quantities, to the different formats, and to the change that will occur.

Future studies should take into account the possibility that the PFC activation, at least for human adults, might not reflect number-specific representation, but other functions that support or utilise numerical representation in the parietal lobes.

10. Abstract after all?

Our primary intention in this article has been to question the idea that the default numerical representation is

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abstract. We need, however, to account for the evidence that points towards abstraction and against our view. Assuming that abstract representation might after all exist under certain conditions, our contention, following Barsalou (2003), is that it occurs as a consequence of the intentional processing of numbers, which leads to explicit creation of connections between different notation-specific representations. We also contend that this cross-talk between notations occurs on-line on a task-by-task basis, but does not exist off-line. We can do no better than Barsalou's words: "abstraction is simply a skill that supports goal achievement in a particular situation" (Barsalou 2003, p. 1184). We therefore suggest that when numerical representation is probed automatically (or implicitly), one will be more likely to find evidence for different numerical representations. However, when researchers use an intentional task, they might encourage the subject to modify the default non-abstract representations. Similar examples can be extracted from the mapping of numbers into space. There is good evidence that we map numbers from left to right as numerical value increases. However, under certain conditions one *can* represent numbers in reverse format, from right to left (Bachtold et al. 1998). Similarly, we argue that humans do not, as a default, represent numbers abstractly, but can adopt strategies that, in response to task configuration and demands, *can* create real or apparent abstraction.

As numerical representation is highly flexible, and not static, what are the neural correlates for such representations? While the IPS shows a consistent modulation for numerical quantity, in different paradigms and labs (Ansari et al. 2006a; 2006b; Castelli et al. 2006; Cohen Kadosh et al. 2005; 2007c; Fias et al. 2003; 2007; Pesenti et al. 2000; Piazza et al. 2004; Tang et al. 2006a; Wood et al. 2006b, for reviews, see Ansari 2008; Brannon 2006; Cantlon et al. 2009; Cohen Kadosh et al. 2008f; Dehaene et al. 2003; Nieder 2005; Walsh 2003), other brain areas outside the IPS also show involvement during numerical processing – for example, the left precentral gyrus (Piazza et al. 2006; Pinel et al. 2004), the right middle temporal gyrus (Cohen Kadosh et al. 2005; Pinel et al. 2001), the right superior temporal sulcus (Cohen Kadosh et al. 2005), the right precentral gyrus (Piazza et al. 2006), the cerebellum (Fias et al. 2003), or the primary visual cortex, and the insula (Piazza et al. 2007). However, aside from the IPS, these areas did not show a consistent activation across studies and tasks. Therefore, the IPS may be the critical part of a distributed and highly interconnected network of regions that gives rise to the representation of numerical magnitude in particular task contexts.

In his dual code hypothesis, Paivio (1971; for extensions see Barsalou et al. 2008; Glaser 1992) suggested that semantic knowledge is represented internally by linguistic (verbal) and imagery (pictorial) codes, which involved internal translation between them. Similar to our view on numerical cognition, he proposed that the involvement of each code depends on the task demands. Generally, whereas picture stimuli tend to activate imagery codes, word stimuli are coded initially by the linguistic codes. Paivio further suggested that the dual code of linguistic and imagistic representations might underlie all of cognitive activities.

Our current cognitive neuro-anatomical approach is partly inspired by cognitive processes as described by the dual code theory and its extensions. Similarly, we propose that dual codes are active during numerical representation. Instead of the terminology of linguistic and imagery codes we use the terminology of automatic and intentional codes, respectively. At the first stage, there is an automatic activation of the numerical quantity that is modality- and notation-specific (similar to the linguistic representations in the Language and Situated Simulation model; for a review, see Barsalou et al. 2008) in the IPS. This processing is crude and not as refined (Banks et al. 1976; Cohen Kadosh 2008b; Tzelgov et al. 1992). Later, the representation of numerical information in the IPS can be further refined. This refinement depends on the time of the activation, intentional processing, task demands, and is resource-dependent. The representation at this stage can be transferred to an on-line representation by a few, the majority, or the entire neuronal population in the IPS, which was activated at an earlier point during automatic numerical representation. This transition from automatic to intentional representation can be subserved by the PFC neural circuitry that is malleable, and its activity reflects learned associations and rules (Duncan 2001) (e.g., that 5 and FIVE have the same quantity) (see Fig. 5). Note, that because dot patterns are considered prelinguistic, the terminology of linguistic code cannot be applied here. As for the imagery code, which according to the dual code hypothesis is pictogram, a tentative suggestion is that in the western culture this will be a digit, as it is the most used pictogram for numbers in the western culture.

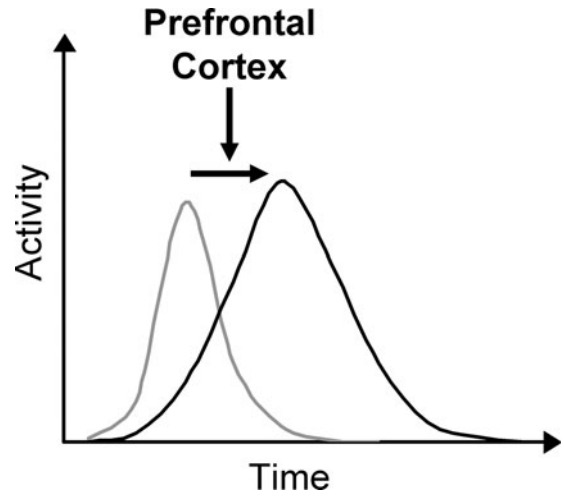


Figure 5. Automatic (gray) and intentional (black) numerical representations. Automatic numerical always precedes the intentional numerical processing. However, the height, shape, and offset of the two distributions are not fixed, and are context- and task-dependent. The transition from automatic to intentional representation in the IPS can be subserved by the PFC neural circuitry that is malleable, and its activity reflects learned associations and rules (Duncan 2001). Note that this division also mirrors the separation of approximate and exact systems with the former being fast and automatic, and the later slow and intentional. This model is similar to the Language and Situated Simulation model, in which the automatic and intentional representations correspond to linguistic and situated simulation systems (Barsalou et al. 2008).

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As the occurrence of automatic processing per se, without intentional processing, is rather limited (Perlman & Tzelgov 2006), the height, shape, and offset of the distributions of the automatic and intentional numerical representations that are presented in Figure 5 are not assumed to be fixed, and are context- and task-dependent. For example, in some tasks the intentional processing can be more dominant than the automatic processing. Thus, the two distributions are only examples and can take place in many different forms, and in some conditions without or with minimal intentional processing. This model can explain the different behavioural and neuroimaging results that we reviewed in favour of non-abstract representations (automatic numerical processing), and those that might imply abstract representation (intentional numerical processing). For example, when the intentional representation is more dominant, there is a need for increasing statistical power in order to uncover the non-abstract numerical representation that occurs during the previous stage and is masked by the intentional processing that creates an on-line abstract representation. In addition, when no intentional processing is needed, the detection of non-abstract representation is easier to observe. Furthermore, this model can further explain the distinct and shared representations for general magnitude in the IPS (Cantlon et al. 2009; Cohen Kadosh et al. 2008f; Walsh 2003), which corresponds in the current case also to automatic and intentional, respectively.

As one of the reviewers pointed out, our terminology of initial automatic processing that is followed by an intentional and deliberate processing with increased precision can profitably extend the positions in the field of conceptual processing as reviewed by Glaser (1992) and Barsalou et al. (2008). In short, Solomon and Barsalou (2004; see Barsalou et al. 2008, for a review of further studies) suggested that when task conditions allow the usage of shallow processing, participants use a superficial linguistic strategy. However, when a deeper conceptual processing is needed they use simulation (imagery), which occurs after the linguistic code. This interplay between linguistic and simulation codes can be modulated by automatic and intentional processing, respectively. Moreover, our terminology helps explain effects in other domains such as in language comprehension, conceptual processing, social processes, and education (for examples, see Barsalou et al. 2008). For instance, children with developmental dyscalculia might experience difficulties in processing numbers because of deficits in automatic numerical processing (Rubinsten & Henik 2005; 2006). According to the current framework, this problem leads to a greater reliance on intentional processing, which leaves, in turn, less resources for manipulations when they are facing more complicated computation, or when they need to learn more advanced strategies (Butterworth 2004). However, one important distinction between our model and other modifications of the dual-code is that our neuro-anatomical framework includes the IPS, a critical area for numerical cognition. Other fields might depend on other brain areas/networks (e.g., temporal structures during language tasks), but we assume that the information processing, namely, the transition from automatic to intentional processing, is based on similar principles.

11. Future directions

The question of specialisation of numerical representation has been relatively neglected, compared to other functions such as face, colour, or object perception (Cohen Kadosh & Johnson 2007). Several possible directions of research can remedy this.

1. *Single-cell neurophysiology.* Following Diester and Nieder's (2007) study, it is important to examine how learning affects numerical representation in the parietal lobe. It might be that after longer training, neurons in the parietal lobe will show activation for both digits and dots. However, following the interactive specialisation approach (Cohen Kadosh & Johnson 2007; Johnson 2001; Johnson et al. 2009), we believe that learning will lead to neuronal specialisation, just as observed with magnitude processing (Cohen Kadosh et al. 2008f; Cohen Kadosh & Walsh 2008; Holloway & Ansari 2008). Another direction will be to use automatic and intentional tasks to examine whether the abstract representation in the prefrontal lobes is a function of natural representation or a result of strategies employed according to task requirements.

• *Developmental studies.* By using habituation paradigms with sequential and simultaneous presentations, it is possible to examine whether infants habituate to the same quantity independent of format. However, one possibility is that the trajectory of numerical representation follows the same principle as other types of magnitude representations (Cohen Kadosh et al. 2008f; Holloway & Ansari 2008), and other brain functions (Cohen Kadosh & Johnson 2007), and follows a trajectory from non-specific to increasingly specialised representations as a function of learning.

III. *Automaticity and intentionality*. The passive task used in different adaptation paradigms also has some limitations; the experimenter cannot know if some subjects decide to attend to and act on the numbers (Perlman & Tzelgov 2006). Studying numerical representation by using automatic processing (e.g., Stroop-like paradigms) can yield a description of the numerical representation that is not dependent on specific task demands. Adopting this approach of contrasting the automatic and intentional processing of numerical information with different notations will yield a better characterisation of the abstract and non-abstract representations, and the conditions under which each representation is activated.

FOUR. *Neuroimaging.* Combination of techniques with good temporal resolution (magnetoencephalography, ERP) and spatial resolution (fMRI) can shed light on the model that we presented in Figure 5. These techniques will allow the detection of the representations under automatic processing, and the interplay between the representation under automatic and intentional representations in the IPS, and the possible recurrent processing from the PFC, in the case of intentional processing. Aside from fMRI, multivariate pattern recognition, an analysis that uses pattern classification algorithms to decode fMRI activity that is distributed across multiple voxels, can also provides a means to disentangle different neuronal substrates as a function of numerical representation.

5. *Neuronal modelling.* Not surprisingly, the issue of non-abstract representation has been neglected, possibly because of the salience and convenience of the view that numbers are

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represented in an abstract fashion. However, a few studies have addressed the issue of abstract representation, at least indirectly. Some of them lead to the conclusion that the properties of numerical representation for dots and digits might not be identical (Verguts & Fias 2004; Verguts et al. 2005). A clear direction for future research in this field is to examine issues such as task-dependent representation, or typical and atypical development of numerical representations as a function of interaction between brain areas (Ansari & Karmiloff-Smith 2002). A great deal is known about the behaviour of numerical systems and we also have good characterisations of the anatomy and functions of key areas to provide constraints on models.

12. Conclusion

The idea that numerical representation is not abstract has, in our view, been cast aside too readily. In contrast, the idea that number representation is abstract has become a premature default position that is not as strongly supported by the evidence on which it is based as its predominance may suggest. Here we have provided evidence from behavioural and neuroimaging studies in humans to single-cell neurophysiology in monkeys that cannot be explained by the abstract numerical representation, as they clearly indicate that numerical representation is non-abstract. It is an open question if numerical representation, at least under certain conditions, is abstract at all. We therefore suggest that before sleep-walking into orthodoxy the alternative idea is revitalised and given further consideration. Future studies should take into account the different methodological and theoretical arguments that we have raised in this target article, before concluding that numerical representation is abstract, as well as any other conclusions regarding the commonalities between processes.

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Open Peer Commentary

Slippery platform: The role of automatic and intentional processes in testing the effect of notation

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Abstract: The type of processing of numerical dimensions varies greatly and is governed by context. Considering this flexibility in tandem with a fuzzy demarcation line between automatic and intentional processes, it is suggested that testing the effect of notation should not be confined to automatic processing, in particular to passive viewing. Recent behavioral data satisfying the authors' stipulations reveal a considerable, though perhaps not exclusive, core of common abstract processing.

In a clearly written and thought provoking article, Cohen Kadosh & Walsh (CK&W) make three interrelated arguments. First, they claim that the meaning of numerals – numerical magnitude – is activated in an automatic fashion just about whenever a numeral is presented for view. Second, they argue that notation-induced differences in processing can be tapped when one does not impose an intentional task, indeed any task, engaging the presented numerals. Third, they suggest that the best behavioral avenue to uncover the effect of notation is to perform Stroop-like conflict studies in which the different notations serve in turn as the target and the to-be-ignored dimensions. The generic view advanced by the authors has merit, but there are difficulties with the arguments.

Concerning the first argument, the authors pinpoint the vast experience that humans have with numbers and conclude that, as a result, numbers are over-learned and processed in an automatic fashion. Numbers are certainly ubiquitous in people's cognitive milieu, but it does not follow that the full arithmetic properties of a number are activated in an obligatory fashion just whenever a number is presented for any purpose. As Stevens noted in his celebrated chapter, a numeral can be "an ink mark on a piece of paper" (Stevens 1951, p. 22); another intellectual giant of quantitative psychology has similarly remarked that numerals can sometimes be mere "scratches on paper" (Guilford 1954, p. 5). Human cognition is a wonderfully adjustable system, flexible enough to treat numerals as mere shapes when that suffices to perform the task (if there is one to perform). This conclusion was reached in a tightly controlled study by Cohen (2009). Cohen presented participants with a single numeral (between 1 and 9) and asked perhaps the simplest possible question: to identify whether the presented numeral was a 5. If numbers automatically activate their magnitude representations, then reaction time should be a function of the distance between 5 and the presented numeral. Instead, magnitude information did not affect the data, only physical shape did. Cohen (2009) concluded that "numerical symbols do not automatically activate quantity representations" (p. 336) and that, in the absence of meaning, the shapes determine the results. Ratinckx et al. (2005) reached similar conclusions with respect to two-digit numerals.

Typical markers of automatic activation mentioned by the authors, such as the size congruity effect, are also inconsistent with a sharp dichotomy between automatic and intentional processing. Virtually all studies that demonstrated the effect (of task-irrelevant numerical magnitude on judgments of physical size) used a design that favored the numerical over the physical dimension in the first place. Thus, more values of number than values of physical size were typically presented (indeed, most studies used merely two values for size: large, small). Moreover, the numerals were easier to discriminate from one another than their physical sizes. When these and further contextual biases were removed (Algom et al. 1996; Pansky & Algom 1999; 2002), the size congruity effect evaporated – with the numbers processed as mere shapes. And, when physical size is made the more salient dimension (Fitousi & Algom 2006) the size congruity effect reverses with physical size intruding on number magnitude more than vice versa. Such pliability is inharmonious with (strongly) automatic processing. The absence of automatic activation of (cardinal) numerical magnitude has been shown with respect to another marker of automatic activation, the SNARC effect (Ben-Nathan et al. 2009). Of even more concern, these two putative markers of automatic activation were unrelated for the same numbers with the same observers (Fitousi et al. 2009).

The upshot is that (a) automatic and intentional processing do not form a dichotomy, but rather, mark the end-points of a finely

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grained continuum, and that (b) the dominant type processing is under strong contextual control. Consequently, numerical magnitude is not activated in an automatic fashion on an unlimited scale; it is not the default processing option when a numeral is presented for view. When contextual demands do not invite number processing, the presented numerals may well be processed as mere shapes or marks. Therefore, it is not prima facie clear what the recordings in the adaptation paradigms with passive viewing signify. They might not be pure measures of number processing (note: numerals in different notation differ in shape). Alternatively, some features (demand characteristics?) of the experimental situation might have invited/encouraged number processing. Be that as it may, passive viewing seems to be a suboptimal vehicle to test notation-induced differences in processing. CK&W seem to admit this when they mention that the experimenter cannot know what aspect of the stimulus the observers elect to attend.

Given the fuzzy demarcation of automatic processing, I do not fully agree with the second claim made by the authors that the effect of notation should be tested via automatic processing. Of course, the authors can retort that, regardless of the generic question of automaticity, the testing can take place in those conditions in which automatic processing has been verified in advance (e.g., a size congruity effect is demonstrated for the stimuli). Note that this stipulation cannot apply with passive viewing. However, I am not convinced that intentional processing is inherently unsuitable for testing the effects of notation. Surely, strategies can bias processing but they do not invariably act to produce a common abstract representation. Thus, Fias (2001) did find a dissociation between a parity judgment task and a phoneme verification task with verbal numbers, even though magnitude information is not needed for performance in *both* tasks. Damian (2004) demonstrated a task-dependent asymmetry in performance across Arabic and verbal numerals. So, I would not rule out intentional processing as platform for testing the question of notational effects.

Concerning the third argument, by a fortuitous coincidence, Ben-Nathan (2009; Ben-Nathan & Algom 2008) performed the experiment recommended by the authors: A pair of numerals appeared on each trial, an Arabic digit and a verbal number, and the participants decided, while timed, whether the number in the target notation was larger or smaller than a standard number. The Stroop effect for each notation was calculated as the difference in performance between congruent and incongruent displays. As the results show (Fig. 1), both Arabic and word performance was affected by the irrelevant number in the alternative notation, although the effect was greater for word. This set of data is not completely decisive, but the Stroop effects recorded for *both* notations tap a considerable amount of common, hence abstract, processing.

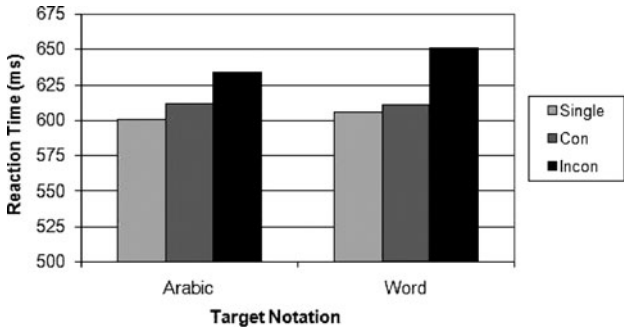


Figure 1 (Algom). The time needed to decide the numerical magnitude (larger or smaller than the standard) as a function of target notation and congruity. [Con: congruent, Incon: incongruent].

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Are non-abstract brain representations of number developmentally plausible?

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Abstract: The theory put forward by Cohen Kadosh & Walsh (CK&W) proposing that semantic representations of numerical magnitude in the parietal cortex are format-specific, does not specify how these representations might be constructed over the course of learning and development. The developmental predictions of the non-abstract theory are discussed and the need for a developmental perspective on the abstract versus non-abstract question highlighted.

In several parts of their target article, Cohen Kadosh & Walsh (CK&W) highlight the importance of taking a developmental perspective in explorations of the brain's representation of number. However, their article does not provide a model of how non-abstract representation of number in the parietal cortex might arise over developmental time. Since many of the representational formats described by CK&W, such as Arabic numerals and number words, are cultural inventions, their brain representation(s) must be the outcome of a developmental process. In other words, the theory raises the question of why development would involve the construction of a system with multiple format-specific representations of numerical magnitude in the parietal cortex?

In this commentary, I explore the notion of non-abstract representations of numerical magnitude from a developmental perspective and contend that currently available theory and evidence suggests that abstract representations of numerical magnitude are a more plausible outcome of development than non-abstract representations.

According to several current theoretical proposals (Dehaene 1997; Verguts & Fias 2004), the acquisition of exact, symbolic representations of number requires the interaction between, on the one hand, preverbal systems that have a long evolutionary history and are shared between species and, on the other hand, language-related, symbolic representation of number that are the product of cultural history. Specifically, evidence suggests that infants and nonverbal animals share the ability to discriminate between large, non-symbolic numerosities (such as arrays of dots), and that infants discrimination abilities are, consistent with Weber's law, ratio dependent (for a review, see Brannon 2006). In addition to this approximate system for the representation of large numbers, infants are thought to have a system for the precise representation of small sets of objects (Feigenson et al. 2004), which is thought to support the ability of children and adults to rapidly (without counting) enumerate small (1–4) items (frequently called "subitizing"). These early representational systems are thought to play an important role in children's acquisition of higher-level numerical skills. In particular, recent evidence suggests that infants' representation of small sets scaffolds their understanding of the meaning of counting (Le Corre & Carey 2007). Subsequent to children's gaining understanding of the meaning of number words, numerical symbols such as Arabic numerals are learnt and presumably these initially meaningless symbols acquire their meaning by being mapped onto corresponding number words, which are in turn mapped onto preverbal systems for the representation of

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numerical magnitude. Thus, development is thought to involve the progressive acquisition of the mappings between different external representations of number. Thus, while the processes that are involved in mapping from external to internal representations may differ between stimulus formats, the internal semantic referent does not differ between representation formats. It is this common representation that allows for the translation between formats. This is also the prediction made by Verguts and Fias, who argue that symbolic and non-symbolic representations of numerical magnitude are mapped onto a shared representation of numerical magnitude subserved by the intraparietal cortex via different pathways. Recent empirical work has supported this proposal by showing format-general representation of quantity in the intraparietal sulcus, as well as format-specific activation in other brain regions (Ansari & Holloway 2008; Santes et al., in press). In other words, format-specificity lies in the process of mapping between, on the one hand, different external representations (i.e., number words to Arabic numerals) and, on the other hand, the mapping between external representation and a common, format-general, internal representation of numerical magnitude. This theory is different from the model put forward by CK&W in which the representation of numerical magnitude itself is predicted to be format-specific.

Given that development is thought to involve the progressive interconnection between different external representations that refer to a common internal representation of numerical magnitude, it seems more plausible that development involves the progressive specialization of the parietal cortex for format-independent rather than format-dependent representations of numerical magnitude, while other brain regions might mediate between representations and subserve the association between each external representation and the common, abstract representation of numerical magnitude.

Indeed, a recent neuroimaging study (Cantlon et al., in press) provides evidence to suggest that both children and adults exhibit common activation of the inferior parietal cortex during the processing of symbolic and non-symbolic numerical magnitude. However, children additionally activate prefrontal regions, which may mediate the association between different formats. Such data are consistent with the interactive specialization model of functional brain development, in which functional brain specialization is the product of the interaction between multiple brain regions (Johnson 2001).

If the proposal by CK&W is indeed correct, then the current models of the development of numerical magnitude representations need to be radically revised. If the semantic representation, for example, of number symbols differs qualitatively from the representation of number words and non-symbolic representations of numerical magnitude, then the development of children's understanding of these external representations must involve independent developmental trajectories. Specifically, different external representations of numerical magnitude would be expected to acquire their meaning independently of one another, rather than through becoming interconnected. Furthermore, this developmental trajectory would differ between speakers of different languages and second-language acquisition would be predicted to involve the construction of a new parietal representation for the number words in the newly acquired language. What are the neurocognitive processes that allow for the construction of these format-specific semantic representations of numerical magnitude? The implications of such independent representations might be that children cannot use their semantic representation of number words in order to understand the meaning of Arabic numerals. Furthermore, this would have educational repercussions and may lead to less focus on the relationships between different formats of representations in the classroom.

Taken together, in its current form, the proposal for non-abstract representations put forward by CK&W does not account for the emergence of non-abstract representations over the course of learning and development. Because different formats for the external representation of numerical magnitude are acquired over the course of learning and development, the non-abstract theory must be put to the developmental test.

Numerical abstractness and elementary arithmetic

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Abstract: Like number representation, basic arithmetic seems to be a natural candidate for abstract instantiation in the brain. To investigate this, researchers have examined effects of numeral format on elementary arithmetic (e.g., 4 + 5 vs. four + five). Different numeral formats often recruit distinct processes for arithmetic, reinforcing the conclusion that number processing is not necessarily abstracted away from numeral format.

Cardinal number is an abstract property of a set of elements because it is invariant for all possible kinds of elements or referents. The basic arithmetic operations (i.e., addition, multiplication, subtraction, and division), at least when viewed as formal arithmetical functions, are similarly abstract because the kinds or referents of problem operands are irrelevant. For this reason, both number and arithmetic seem to be natural candidates for abstract instantiation in the brain. Not surprisingly, then, the issue of abstraction has engaged cognitive arithmetic researchers in much the same debate that has occupied research on quantity representation. In the target article, Cohen Kadosh & Walsh (CK&W) have focused on effects of numerical format (e.g., 4 vs. four) in tasks that directly or indirectly tap quantity processing, but they have not discussed in any detail the substantial body of research that has examined effects of numeral format on elementary arithmetic (e.g., 4 + 5 vs. four + five).

In fact, the prominent models of number processing advocated by Dehaene et al. (1998a) and McCloskey and Macaruso (1995), which assume that different numeral formats activate a common quantity representation, similarly assume that elementary arithmetic is abstracted away from surface form (see also Venkatraman et al. 2005). Alternatively, cognitive processes for arithmetic could vary with format (see Campbell & Epp [2005] for a review of relevant literature). In this alternative view, there are two senses in which elementary arithmetic could be non-abstract. First, calculation performance could be based on discrete, format- and operation-specific processes (McNeil & Warrington 1994). This implies non-abstract representation in the same sense defined in the target article (i.e., different formats recruit distinct neuronal populations). Second, calculation might be based on overlapping representations across formats, but calculation efficiency is format specific. This would occur if problem-encoding processes and calculation processes were interactive rather than strictly additive (Szűcs & Csépe 2004). As the following paragraphs illustrate, there is evidence that performance of elementary arithmetic by educated adults is non-abstract in both senses.

In experimental research examining format effects on elementary calculation, the most common contrast has involved arithmetic problems in Arabic digit format (5 + 6) versus written word format (five + six). It is consistently found that performance is much slower and more error prone with written-word operands compared to Arabic digits. Campbell and Epp (2005)

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proposed that relatively poor performance with arithmetic problems in written-word format occurs because number-fact retrieval processes are less efficient with word compared to digit operands. Arithmetic problems are encountered more frequently in digit format (e.g., $2 + 6$, 4×5) than in written number-word format (two + six, four × five). Consequently, digit problems are more likely to activate a visual retrieval path than would a written-word problem (McNeil & Warrington 1994). Retrieval, given number words, presumably requires phonological recoding of problems so that the proximal retrieval cue is based on auditory-phonological codes. Retrieval with digits, therefore, would be more efficient because it is mediated both by well-established visual and phonological routes, whereas retrieval with number-word format would not provide a direct visual basis for retrieval.

The proposal that arithmetic-fact retrieval efficiency is lower with problems in word format than digit format is also supported by the well-replicated finding that non-retrieval strategies (i.e., procedural strategies such as counting or decomposition) are reported more often given word format (six + seven) than digit format (6 + 7) (Campbell & Epp 2005). Educated adults report procedural strategies for simple arithmetic up to 50% more with problems in written-word format than digit format (Campbell & Alberts, in press). Format-induced strategy shifts imply that different formats often recruit different neural processes for elementary arithmetic. Indeed, imaging research suggests that retrieval of arithmetic facts is associated with linguistic representations in the left angular gyrus, whereas procedural strategies requiring semantic quantity processing recruit bilateral components of the intraparietal sulcus (Dehaene et al. 2004). As direct retrieval and procedural strategies activate distinct brain regions (see also Dehaene et al. 2003), the effects of format on strategy choice for elementary arithmetic imply that calculation is not generally abstracted away from surface form.

Format-related strategy shifts demonstrate that calculation performance sometimes involves discrete, format-specific processes, but calculation also appears to be non-abstract in the second sense mentioned earlier; namely, that format-specific encoding processes or context can interact with calculation processes. One source of evidence for this comes, again, from research examining format effects on simple arithmetic: When procedural strategy trials are removed from analysis and only retrieval trials are analyzed, there remain substantial word-format costs relative to digit format, and word-format retrieval costs tend to increase with problem difficulty (Campbell et al. 2004; Campbell & Penner-Wilger 2006). This reinforces the conclusion that arithmetic retrieval processes are not abstracted away from surface format.

The non-abstractness of elementary arithmetic is demonstrated further by context-dependent activation of arithmetic facts. Bassok et al. (2008) found evidence for obligatory activation of addition facts ($4 + 2 = 6$) when problems were primed by word pairs semantically aligned with addition (e.g., tulips-daisies, which afford addition as a collection of flowers), but not when they were primed by pairs misaligned with addition (hens-radios, records-songs). The automaticity of arithmetic fact retrieval thereby depended on the analogical consistency of the semantic context activated by the prime and the specific arithmetic operation to be performed. This implies that the kinds and referents of problem operands are relevant to cognitive arithmetic, despite being irrelevant to arithmetic as a formal operation. Like the effects of surface form, semantic alignment phenomena demonstrate that cognitive arithmetic is not abstracted away from the conditions of problem encoding. Research on elementary arithmetic thereby aligns with the theoretical perspective represented in the target article, and points toward integrated, multimodal mechanisms in favor of abstract or amodal representations and processes (e.g., Barsalou 2008; Clark & Campbell 1991).

Numerical abstraction: It ain't broke

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Abstract: The dual-code proposal of number representation put forward by Cohen Kadosh & Walsh (CK&W) accounts for only a fraction of the many modes of numerical abstraction. Contrary to their proposal, robust data from human infants and nonhuman animals indicate that abstract numerical representations are psychologically primitive. Additionally, much of the behavioral and neural data cited to support CK&W's proposal is, in fact, neutral on the issue of numerical abstraction.

Cohen Kadosh & Walsh (CK&W) propose a new dual-code model of numerical representation that posits a psychological and neural distinction between fast, automatic notation-dependent representations and slower, intentional notation-independent representations. In their model, notation- and modality-specific (non-abstract) representations are psychologically more primary than abstract representations. We argue that this proposal is limited in its psychological and neurobiological perspective on numerical abstraction, and that the evidence they offer is either neutral on the issue of whether numbers are represented abstractly, or equally compatible with existing models of number representation.

A central limitation of CK&W's proposal is the coarse manner in which it surveys the theoretical landscape of numerical abstraction. At the psychological level, numerical abstraction can refer to notation independence, modality independence, or the representation of number independently of dimensions such as time, space, size, and color. For instance, the capacity to recognize that a group of three elephants is equal in number to a group of three umbrellas, but that both are fewer in number than a series of ten gunshots, is a feat of numerical abstraction. We know from scores of behavioral studies that human infants and nonhuman animals smoothly represent non-symbolic numerical values across modalities and dimensions (e.g., Cantlon & Brannon 2006; Church & Meck 1984; Hauser et al. 2002; Jordan & Brannon 2006; Jordan et al. 2005; 2008; Kobayashi et al. 2005; Nieder et al. 2006; Starkey et al. 1983; Wood & Spelke 2005). Importantly, infants and nonhuman animals exhibit these abstract numerical representations in the absence of symbolic language, and they do so spontaneously. Thus, numerical representations can be abstract in the absence of discrete symbolic representations or explicit task demands. CK&W's claim that "numerical representation is primarily non-abstract" (target article, Abstract) and that intentional processing is required to achieve notation- and modality-independent representations of numerical values is at odds with the demonstrated existence of this non-symbolic form of numerical abstraction.

Abstract non-symbolic numerical representations are important to any theory of numerical representation because they are hypothesized to provide the evolutionary and developmental foundation upon which symbolic numerical representations are psychologically constructed (e.g., Carey 2004; Gallistel & Gelman 2000). In other words, current developmental and evolutionary theories propose that numerical representations are abstract before they are symbolic. Therefore, CK&W's proposal needs to either (1) provide a theoretical account of the alleged developmental disappearance of automatic numerical abstraction in human children, or (2) make the case that preverbal infants and nonhuman animals spontaneously engage in intentional processing to represent numerical values across modalities and dimensions.

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A second theoretical limitation of CK&W's proposal is that their neurobiological definition of numerical abstraction risks *reductio ad absurdum*. That is, the stipulation that numerical abstraction requires identical responses in identical neurons is potentially impossible to satisfy. Yet, even if it were possible to satisfy that criterion, it is not clear whether it is the appropriate criterion for establishing numerical abstraction. As the authors review, regions of the intraparietal sulcus (IPS) respond during numerical processing across notations, modalities, and dimensions. The mounting evidence that numerical representations across notations, modalities, and dimensions are "distributed but overlapping" in the IPS is neutral on the issue of whether the underlying representations are abstract. Instead, such evidence suggests that different numerical forms invoke both shared and separate neural processes. CK&W's conclusion that the neurobiological data weigh more heavily in favor of notation-dependent neural processes is therefore merely an assertion at this stage.

Other empirical evidence that CK&W cite in favor of their account does not do the theoretical work the authors are asking of it. The authors review both behavioral and neurobiological evidence purportedly revealing notation-specific interactions in numerical tasks. However, many of the notation-specific interactions they review hinge on generic differences in performance level. Specifically, if a single psychological process is involved in judging numerical values from two different numerical notations (e.g., numerical judgments of Arabic numerals and arrays of dots), yet the judgment is easier for one of the two notations (e.g., because the input mode is more rapid, reliable, or fluent), a notation-specific interaction may emerge simply because performance on the easier notation hit ceiling accuracy or floor speed. Such interactions, though cited by CK&W, do not invite the theoretical implications that CK&W draw. Instead, notation- or modality-specific interactions that arise under these circumstances reflect a quantitative difference in performance between notations or modalities. Note that this argument may also apply to neurobiological findings under circumstances in which floor or ceiling response levels are achieved. While bearing this issue in mind, we encourage CK&W to re-evaluate the relevance of the following studies to their argument for notation- and modality-dependent number representations: Dehaene and Akhavein (1995), Droit-Volet et al. (2008), Ganor-Stern and Tzelgov (2008), Hung et al. (2008), and Ito and Hatta (2003). These studies (and likely others) report interactions that do not necessarily support a notation- or modality-dependent account of numerical representation.

Importantly, any notation- or modality-dependent interaction that survives inspection for a generic performance effect likely can be accounted for by the two-system view of approximate and exact numerical representation proposed by Dehaene et al. (1999). In the pre-existing two-system proposal, notation-specific interactions may arise from an interplay between the exact and approximate numerical codes. Unfortunately, CK&W have not distinguished the empirical predictions of their dual-code view from the existing two-system view.

In short, although we applaud CK&W for highlighting some of the many remaining puzzles about the nature of numerical abstraction in the mind and brain, the solutions they offer do not adequately account for the data. Moreover, the open questions surrounding the cognitive and neural basis of numerical abstraction do not warrant a restructuring of the field of numerical cognition. Robust evidence demonstrates that with or without language, number is represented abstractly – independently of perceptual features, dimensions, modality, and notation. In fact, this is the very definition of "number."

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Numerical representations are neither abstract nor automatic

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Abstract: In this commentary, I support and augment Cohen Kadosh & Walsh's (CK&W's) argument that numerical representations are not abstract. I briefly review data that support the non-abstract nature of the representation of numbers between zero and one, and I discuss how a failure to test alternative hypotheses has led researchers to erroneously conclude that numerals automatically activate their semantic meaning.

There exists in the numerical cognition literature what I call the triple tautology: that numerical representations are (1) *automatically activated*, (2) *abstract*, and (3) *analogue*. Cohen Kadosh & Walsh (CK&W) present a convincing argument that numerical representations are not abstract. Although CK&W focus on the numerical representation of integers, strong evidence also exists for the non-abstract nature of the numerical representation of quantities between zero and one (Cohen et al. 2002). My colleagues and I have shown that, although most college students understand the correct ordinal relation of numbers expressed in a single numerical format (e.g., decimals), they do not understand the correct ordinal relation of numbers expressed in different formats (e.g., comparing decimals to relative frequencies). If the numerical representation of numbers between zero and one were abstract, the students should have been able to compare the semantic meaning of numbers expressed in different numerical formats once the numbers were converted into the abstract representation. Although researchers may discount this evidence for non-abstract representation of numbers as unique to those between zero and one, CK&W reveal that it is consistent with the evidence for the representation of integers.

The crux of CK&W's argument is that correlations should not be confused for causal mechanisms – no matter how intuitive the causal relations may appear. Below, I describe how the remaining two tautologies (automatic activation and analogue representation) also rely heavily on correlational evidence.

It can be argued that Moyer and Landaur (1967) started the modern study of numerical cognition with their discovery of the *numerical distance* effect. In short, the authors presented two integers side-by-side and asked participants to judge which integer was the larger of the two. The authors found that reaction time (RT) varied as a function of the numerical distance between the two presented integers. The robust nature of the finding, together with its appeal to our intuition about the importance of numerical distance, has made this finding one of the bedrocks of the numerical cognition literature. The numerical distance effect was the foundation of the first tautology of numerical cognition: the analogue nature of the representation.

The numerical distance effect is not only the foundation of the first tautology, but it is also a foundation of *automaticity*. A strong test of the automatic activation hypothesis is a simple task in which participants are to judge whether two numerical symbols are the same or different. In previous versions of this task, researchers dichotomized the stimuli into "close" and "far" groups by choosing numbers that are numerically "close" (e.g., 8 and 9) and numbers that are numerically "far" (e.g., 1 and 9). If semantic meaning is automatically activated, it will interfere with participants' same/different judgments and evidence for the numerical distance effect should be present in the RT data. Specifically, the time for participants to judge two numerically close numbers as different (i.e., the "close" group) should be longer than the time it takes them to judge two numerically distant numbers as different (i.e., the "far" group). This is

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exactly what researchers found (Dehaene & Akhavein 1995; Ganor-Stern & Tzelgov 2008), and they reasonably concluded that numerical symbols automatically activated their semantic meaning.

Researchers should remember that, despite its name, the *numerical distance effect* is correlational. That is, numerical distance is one of several features that are correlated with the order of the numbers on the number line. Therefore, although numerical distance is correlated with participants' RTs, it may not be the controlling factor of participants' RTs. As with all correlational data, there may be a third variable that (1) is correlated with numerical distance and (2) is the true controlling factor of participants' responses. The first step in determining whether a third variable exists is to test alternative hypotheses. Unfortunately, in numerical cognition research, researchers rarely (if ever) consider plausible alternatives to the numerical distance hypothesis. Recently, I did just that when I tested whether numerical symbols automatically activate their representation.

I ran the numerical same/different task with two simple changes: (1) I did not dichotomize the stimuli, and (2) I tested an alternative hypothesis. By not dichotomizing the levels of the independent variable, I reduced the number of plausible alternative hypotheses that could explain the data. The plausible alternative I tested was simple: RT increased as a function of the *physical similarity* between the two numbers to be distinguished. See Cohen (2009) for the operational definition of the physical similarity function. The data were clear: Physical similarity was the controlling factor in participants' RTs, not numerical distance. Because the semantic meaning did not interfere with participants' response, the data demonstrated that integers do not automatically activate their semantic meaning. *Because the numerical distance function correlates highly with the physical similarity function* ($r = .62$), *researchers may easily confuse the effects of physical similarity for those of numerical distance if they do not actively test both*.

CK&W benefit the numerical cognition community by reviewing the literature addressing the abstract nature of numerical representations. The authors remind us not to confuse correlations for causal mechanisms. I echo that sentiment and remind readers that the numerical distance effect is, at its essence, simply a correlation. By challenging the tautologies of the field with plausible alternative hypotheses, researchers like Cohen Kadosh & Walsh keep the numerical cognition field moving forward.

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The case for a notation-independent representation of number

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Abstract: Cohen Kadosh & Walsh (CK&W) neglect the solid empirical evidence for a convergence of notation-specific representations onto a shared representation of numerical magnitude. Subliminal priming reveals cross-notation and cross-modality effects, contrary to CK&W's prediction that automatic activation is modality and notation-specific. Notation effects may, however, emerge in the precision, speed, automaticity, and means by which the central magnitude representation is accessed.

Cohen Kadosh & Walsh (CK&W) revive a twenty-year-old proposal in numerical cognition, according to which our capacity for abstract mathematical thought results from a complex interaction of multiple concrete notation-specific codes (Campbell & Clark 1988). Their conclusions, unfortunately, result from discarding of solid empirical evidence supporting a convergence of notation-specific representations onto a shared representation of numerical magnitude, in favor of weak evidence for notation effects. Thus, their article consists in a catalogue of findings in which any difference or interaction involving number notation is taken as strong support for the notation-specific view. In this commentary, I first return to the evidence for notation-independent representations, then discuss interesting reasons why notation occasionally influences brain and behavior.

Evidence for notation-independent number processing. CK&W cite, but do not seem to draw conclusions from, the many functional magnetic resonance imaging (fMRI) studies that have observed shared fMRI activations across different notations for numbers. Most important, are studies showing cross-notation fMRI adaptation, because they cannot be dismissed as just showing activation overlap, or as resulting from artifacts of response selection (Jacob & Nieder 2009; Naccache & Dehaene 2001a; Piazza et al. 2007). As an example, extending earlier work by Piazza et al. (2007), Jacob and Nieder (2009) recently demonstrated that after adaptation to a fraction expressed with Arabic numerals (e.g., 1/2), anterior intraparietal sulcus (IPS) shows a distance-dependent transfer of adaptation to number words (e.g., half). As a second example, Figure 1 replots the data in Naccache and Dehaene (2001a), showing that IPS activation is reduced whenever the same numerical quantity is repeated, regardless of whether notation is changed (Arabic digits vs. number words). Note that in this experiment, the first presentation of the number was subliminal, and yet the results showed clear cross-notation convergence. In general, it is surprising that CK&W do not cite the extensive behavioral literature on subliminal priming demonstrating clear notation-independent effects (e.g., Dehaene et al. 1998b; Reynvoet & Brysbaert 2004; Reynvoet et al. 2002). Even cross-modal subliminal priming was recently demonstrated, from a subliminal Arabic numeral to a conscious spoken numeral (Kouider & Dehaene, in press). These effects argue directly against CK&W's proposal that when numerical representations are probed implicitly, convergence across notations does not occur.

Equally impressive are electrophysiological studies showing that some single neurons, particularly in prefrontal cortex, respond identically to symbolic and various non-symbolic displays of number, with the same exact tuning curve across the interval of numbers tested (Diester & Nieder 2007; Nieder et al. 2006). Astonishingly, CK&W dismiss these beautiful data with the claim that the animals are using a "similar response strategy," for example, for digit 1 and dot 1 compared to other numbers – not acknowledging the fact that their interpretation would require as many putative strategies as there are numbers!

Returning to fMRI, another method that is likely to play a strong role in the coming years is multivariate decoding, which probes fMRI activation for the presence of decodable patterns and their generalization to novel experimental conditions. Using this technique, with Evelyn Eger (Eger et al., submitted), we recently demonstrated that human IPS signals can be used to decode which number a participant is temporarily holding in mind. When trained with Arabic numerals, the IPS decoder generalizes to dot patterns, indicating the presence of an underlying notation-independent neuronal population. Likewise, with André Knops (Knops et al. 2009), we found that a classifier trained with posterior IPS activation during left versus right saccades could spontaneously generalize to a classification of subtraction versus addition trials, whether these calculations were performed with non-symbolic sets of dots or with symbolic Arabic numerals.

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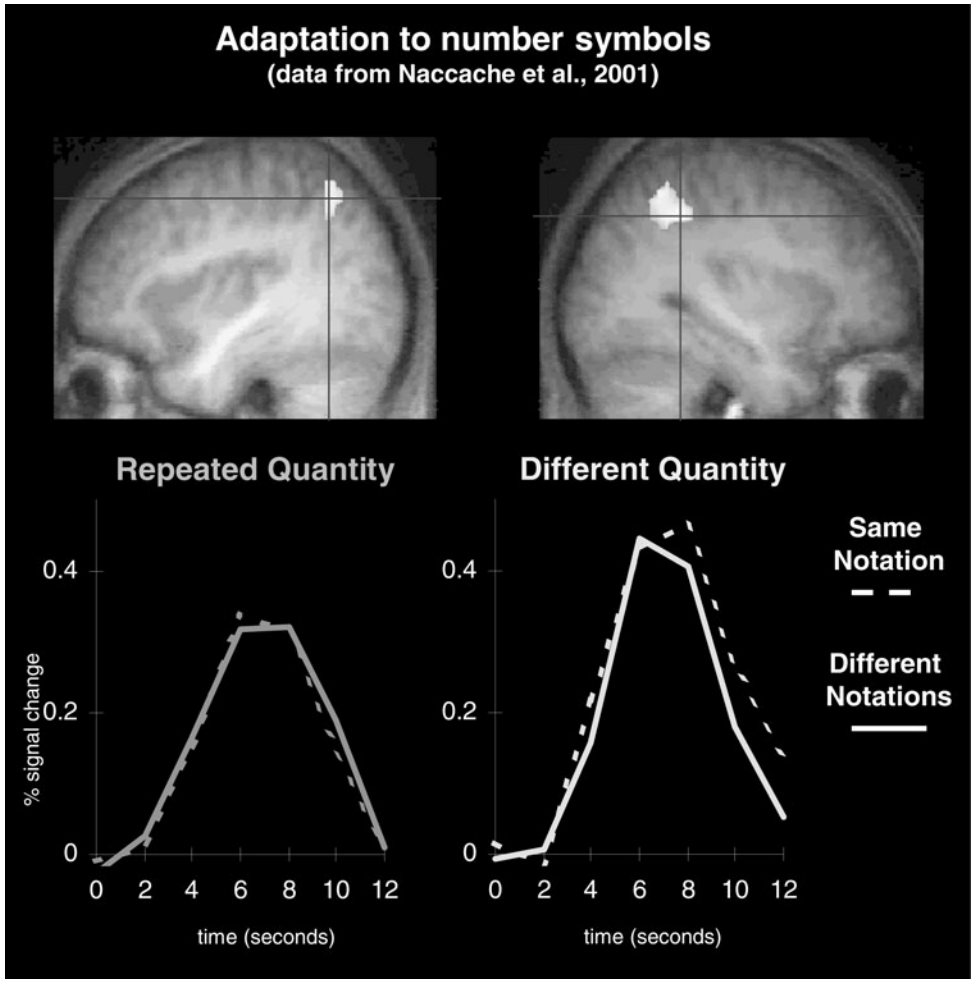


Figure 1 (Dehaene). Evidence for cross-notation subliminal priming and access to a shared representation of Arabic and verbal numerals. Naccache and Dehaene (2001a) presented a subliminal prime prior to each target number in a number comparison task. Using whole-brain fMRI, repetition suppression was observed only in bilateral intraparietal cortex: Trials in which the primes and targets corresponded to the same quantity yielded reduced activation compared to trials in which the quantities differed. Response times were also accelerated by subliminal repetition. In both fMRI and behavior, it made no difference whether the prime and the targets appeared in the same or different notations. Reynvoet et al. (2002) later expanded this work by showing that the amount of priming in response times varies continuously as a function of the numerical distance between the prime and target.

The concept of "abstract representation" is never defined by CK&W, and here the Knops et al. (in press) findings point to an important theoretical point: A representation may be shared across numerical notations, and yet rely on a spatial, non "abstract" format of representation. Knops et al. show that the putative human homolog of monkey area LIP, a retinotopic region involved in attention and eye movement, is partially co-opted for symbolic *and* non-symbolic arithmetic on the number line – a clear instance of "cortical recycling" of a sensorimotor area for a more abstract mathematical use (Dehaene & Cohen 2007).

Interesting reasons why number notation occasionally influences brain and behavior. If numbers presented in various notations contact unified representations of magnitude and space, then why are significant notation effects occasionally observed? Several explanations can be proposed, none of them requiring a hasty dismissal of notation-independent representations.

1. *Numerical precision.* Neural network simulations suggest that the introduction of symbolic representation can lead to a refined precision of the tuning curves for number (Verguts & Fias 2004). Importantly, according to this view, the *same* neurons remain responsive to both symbolic and non-symbolic presentations – only their accuracy changes. Mathematical developments of this theory (Dehaene 2007) suggest that it has the potential to explain many of the known effects of education to symbols on mental arithmetic, including the linearization of number-space mappings (Dehaene et al. 2008; Siegler & Opfer 2003), the improved accuracy with which Arabic numerals can be compared or combined into calculations, and the spontaneous competence of young children when symbols are first introduced (Gilmore et al. 2007) – an effect hard to explain without assuming cross-notation convergence.

2. *Speed and automaticity.* There is no reason to expect all number notations to be equally fast and automatic in accessing the shared magnitude representation. On the contrary, identification is slower for number words than for Arabic numerals. In number comparison, interactions between the distance effect and the verbal versus Arabic notation of the targets can be attributed to a word-length effect unique to written words (Dehaene 1996). Education and over-training also play a role – as children get older, increasingly automatic effects of numerical magnitude are seen, particularly with Arabic numerals (Girelli et al. 2000). These notation effects occur at a perceptual or transcoding level and are largely irrelevant to the existence of a shared central representation for number.

3. *Neural machinery for transcoding.* In the course of converting from a notation-specific neural code to a numerical magnitude code, it is likely that the brain requires special neural

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machinery, possibly including neurons that are attuned to both quantity *and* notation. Indeed, in parietal cortex, neurons with a joint sensitivity to multiple parameters (e.g., eye position *and* retinal location) are frequently recorded and are thought to play a compulsory role in transcoding to and from pure representations of each parameter (Pouget et al. 2002). Similarly, neurons simultaneously tuned to both numerical magnitude and notation (e.g., simultaneous dots vs. serial flashes [Nieder et al. 2006]; or dots versus Arabic symbols [Diester & Nieder 2007]) may play a key role in accessing a common magnitude representation via different routes. Identifying the numerosity of a set of dots may require special neural machinery for summing size-invariant representations of object locations (Dehaene & Changeux 1993), potentially explaining both the existence of neurons monotonically tuned to non-symbolic numerosity in area LIP (Roitman et al. 2007) and the specific form of behavioral priming observed with dots compared to Arabic numerals (Roggeman et al. 2007).

Conclusion. Considerable evidence points to a notation-independent representation of number in the monkey and human IPS. It would, however, be wrong to think of this representation as a "module." First, it does not involve a dedicated area, but only a fraction of IPS neurons, highly distributed in the IPS, and intermingled with other representations of extent, time, location, and other continuous parameters (Pinel et al. 2004; Tudusciuc & Nieder, 2007). Second, it is not "encapsulated," but communicates broadly with other areas, thus allowing humans to attach arbitrary spoken and written symbols to it. Because it acquires its "abstract" character, in large part, through education to number symbols, it is not surprising that notation effects are occasionally seen. Such effects should not divert from the incontrovertible fact that arithmetic, like much of mathematics, consists in the manipulation of internal conceptual representations that abstract away from the specific format of input.

Concrete magnitudes: From numbers to time

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Abstract: Cohen Kadosh & Walsh (CK&W) present convincing evidence indicating the existence of notation-specific numerical representations in parietal cortex. We suggest that the same conclusions can be drawn for a particular type of numerical representation: the representation of time. Notation-dependent representations need not be limited to number but may also be extended to other magnitude-related contents processed in parietal cortex (Walsh 2003).

Number (Piazza et al. 2004) as well as time (Rao et al. 2001) have been found to be represented in the intraparietal sulci (IPS). The mode of their representation – abstract or not abstract – is put into question by evidence uncovered by Cohen Kadosh & Walsh (CK&W). The authors define *abstract* representation as the insensitivity of neuronal populations coding numerical quantity to the notation in which the numerical quantity was presented. CK&W elegantly show in their careful scrutiny of existing studies that this property cannot be attributed to all representations of number. We suggest that their conclusion may be extended to representations of time.

We will refer to representations that are notation-specific as *concrete* representations. We will argue that primary neuronal representations of time (which we speculate may also be found in IPS) could be concrete. CK&W take as their measure of concreteness, the interaction of variations in behavioural data or neuronal activation with different numerical notations. We will show that comparable interactions are found in behavioural performance relating to notation- and modality-specific representations of time. First, we describe some studies that suggest that the representations of number we use to tell the time from clocks are concrete. Second, we will discuss studies that suggest that duration perception may also be concrete.

In a study of clock reading behaviour in children, Friedman and Laycock (1989) found an interaction effect. They asked 6- to 11-year-old children to detect the time displayed in pictures of analog and digital clocks. The success at reading the time from analog displays systematically varied with presented time, but this was not the case for digital displays. The independent variation in performance supports a view of representations of clock time as concrete.

Clock time also seems to be represented concretely in adults. Goolkasian and Park (1980) also found an interaction of notations with presented time. They asked subjects to compare clock times presented as words, with a second clock time presented either in analog or digital notation. There was an effect of the angular distance between the two times if the second stimulus was a clock face as compared to a digital display. This corroborates the finding by Friedman and Laycock (1989) in children and shows that concrete representations of clock time do not disappear during development.

Support for concrete representations of clock time also comes from repetition priming tasks. In a study by Meeuwissen et al. (2004), participants had to name the time from analog clocks, followed by naming the time from a digital clock. Although there was no obvious repetition priming effect with respect to the hour, there was a facilitation present for naming the minutes. If subjects used an abstract representation to name the hour, we would expect to find a priming effect. The absence of such a priming effect suggests that the representations used in naming the hour are concrete. The authors interpreted this finding as evidence that we use different strategies to determine the hour, depending on whether we are using an analog clock or a digital display. Since determining the hour is the first stage in telling the time, we conclude that at this first stage, concrete representations of clock time are employed. Meeuwissen and colleagues showed that once the hour is known, determining the distance in minutes from the hour (e.g., 5 minutes before or after an hour) relies on the same operation for both display formats. This two-stage account of the processing of clock time is consistent with the model CK&W advance concerning the possibility of transformation of primary concrete numerical representations in parietal areas into a common format depending on task demands.

Representations of clock time seem to exert notation-dependent effects on behaviour. We propose that comparable interaction effects can also be found for duration perception, suggesting that the brain may represent temporal intervals concretely. Smith et al. (2007) employed a duration bisection procedure to examine interval timing of two different temporal ranges, 100–500 msec and 1–5 sec, in patients with Parkinson's disease and healthy controls. The authors found a significant interaction between the temporal ranges and modality (visual vs. auditory). Both patients and controls overestimated visual short durations and underestimated visual long durations, but this effect was not observed in the case of auditory durations. This pattern in performance suggests that duration perception is modality-specific, hence concrete.

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Further support for this conclusion comes from the following auditory duration judgment task (Wearden et al. 2007). Participants were presented with a standard stimulus and a comparison stimulus consisting of filled or unfilled auditory durations, and they had to judge if the two stimuli had the same duration or different durations. There were four conditions, filled following unfilled (UF) durations, unfilled following filled (FU), filled following filled (FF), and unfilled following unfilled (UU) durations. The temporal generalisation gradients (i.e., functions plotting the proportion of "same duration" answers over duration differences between standard and comparison stimuli) showed slightly but significantly different shapes for FF trials compared to UU trials and markedly different shapes between FU and UF trials (see Fig. 1). These findings suggest that different notations of auditory stimuli can take distinct processing forms in the brain, providing additional support for the claim that durations are represented concretely.

In conclusion, the reported evidence suggests that not only number, but also time can be represented concretely in the brain. This shared characteristic is in line with the idea of a general magnitude system, which codes time, space, and quantity (Walsh 2003). Both CK&W's and our evidence strongly suggest that a general magnitude system could code different forms of magnitude using concrete representations.

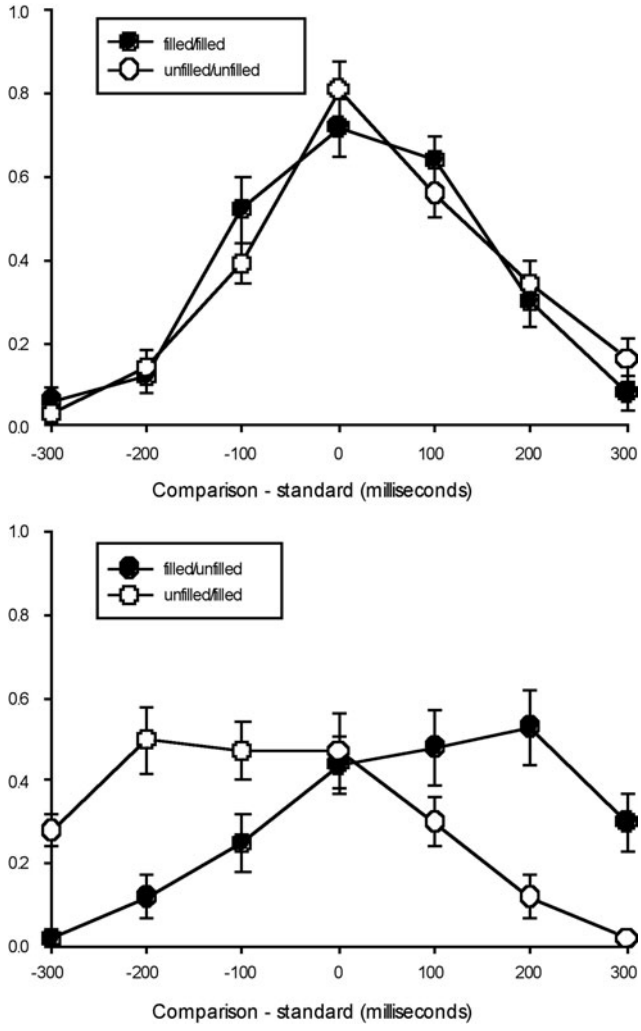


Figure 1 (Falter et al.). Temporal generalisation gradients (mean proportion of "same duration" responses plotted against duration differences between standard and probe stimuli) for comparing filled and unfilled auditory durations. Upper panel: Comparison of filled durations (black circles) versus comparison of unfilled durations (white circles). Lower panel: Filled standards followed by unfilled probes (black circles) versus unfilled standards followed by filled probes (white circles). (Figure from Wearden et al. 2007.)

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Brain neural activity patterns yielding numbers are operators, not representations

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Abstract: We contrapose computational models using representations of numbers in parietal cortical activity patterns (abstract or not) with dynamic models, whereby prefrontal cortex (PFC) orchestrates neural operators. The neural operators under PFC control are activity patterns that mobilize synaptic matrices formed by learning into textured oscillations we observe through the electroencephalogram from the scalp (EEG) and the electrocorticogram from the cortical surface (ECoG). We postulate that specialized operators produce symbolic representations existing only outside of brains.

Cohen Kadosh & Walsh (CK&W) define representations as: "patterns of activation within the brain that correspond to aspects of the external environment" (sect. 2, para. 2). They "differentiate representation from processing" that includes "pre-representation (e.g., visual identification of the digit) and post-representation components (e.g., working memory, response selection)" (sect. 2, para. 2). Thereby, CK&W "argue that the PFC [prefrontal cortex] is not involved in numerical representation, at least not in humans. The PFC is important for some numerical *operations*, but not representations" (sect. 9, emphasis theirs). Figure 5 reflects their view that numerical representations depend on environmental cues that are "coded" initially in "linguistic and imagistic representations." The neural populations in the parietal area provide early "automatic numerical representation," which later transitions to "intentional representation subserved by the PFC neural circuitry."

The authors' distinction between abstract versus non-abstract depends on their restriction of "early representation" to the firings of populations of parietal neurons that are induced or evoked by sensory inputs, and that are revealed by single neuron recordings and areas of functional magnetic imaging (fMRI) activation, while excluding "operations" performed on those populations by the PFC or other parts of the brain.

We share CK&W's views that the direct route to understanding how brains do numbers is by study of activity patterns of the neural populations in question. On experimental grounds, we do not accept their hypothesis that the patterns can be detected by microscopic units, because the numbers of neurons observed by present methods are too few, or by macroscopic fMRI images, because the time scales are too slow. We believe that the patterns will be found, if ever, in mesoscopic brain waves (EEG, EcoG, and the magnetoencephalogram from magnetic sensors fixed around the head [MEG]), which provide the requisite temporal and spatial resolutions (Freeman et al. 2009).

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On theoretical grounds, we do not agree that the patterns are representations, because the mesoscopic wave patterns, which we have observed to accompany sensation and perception of invariant conditioned stimuli, lack invariance; the patterns change with variations in context and experience. We hypothesize that our observed patterns are mesoscopic *operators* in the form of synchronized neural oscillations in the beta and gamma ranges, which map the connection patterns in cortical synaptic networks shaped by learning into spatiotemporal patterns of amplitude modulations. We see the concept of representations as a carry-over from Cartesian dualism, which presupposes the primacy of stimuli as determinants of percepts. No, the primary determinants are memories.

Certainly the firings of neurons, when they are appropriately averaged with respect to time and place of repetitive stimulus onset, manifest the presentations of receptor input into cortex, which differ across trials. Sensory-driven and motor-related microscopic activity reported by the authors in the parietal lobes is consistent with the consequences of lesions in the right parietal lobe, first described by Gerstmann (1958): the syndrome of inability to distinguish left from right (disorientation); difficulty in writing (dysgraphia); difficulty with arithmetic (dyscalculia); and inability to name the digits (finger agnosia). The syndrome suggests that skills in elementary arithmetic are closely tied to intentional actions involving use of the hands in symbolic communication that preceded the emergence in evolution of numerical skills (Freeman 2009). These data support the authors' opposition to abstract representation, but the units are too close to the tactical sensorimotor operations of counting and too far from the conceptual strategic operations of arithmetic.

In our view, perception begins with intention and not with sensation. The capacities to foresee a goal, to plan action to achieve it, and to predict the sensory consequences of the action in mammals clearly involve the PFC in the prior structuring of the wave operators in recall of experience. We believe that all species construct neural operators that direct the body in the action-perception cycle (Merleau-Ponty 1942/1963). What distinguishes humans is the capacity to construct hypothetical meta-operators that combine and reshape the ordinary wave packets that we share with other mammals and make symbols. These representations are in, on (e.g., tattoos), or outside the body, serving social planning and communication.

It is easy to suppose that brains work the way computers do, but the metaphor fails. The mathematician John von Neumann wrote:

> Thus the outward forms of *our* mathematics are not absolutely relevant from the point of view of evaluating what the mathematical or logical language *truly* used by the central nervous system is. . . . It is characterized by less logical and arithmetical depth than what we are normally used to. . . . Whatever the system is, it cannot fail to differ considerably from what we consciously and *explicitly* consider as mathematics. (von Neumann 1958, pp. 81–82)

It is likely that the hypothetical symbol-making operators provide the substrate for both words and numbers. How they differ from the ordinary operators is not known. We think that they are not local operators of the kind postulated by CK&W; instead, they are carried by the patterns of activity that cover wide regions in intermittent spatially coherent oscillations (Kozma & Freeman 2008), which are seen in EEG (Freeman et al. 2003; Pockett et al. 2009; Ruiz et al. in press), ECoG (Freeman et al. 2003), and MEG (Bassett et al. 2008). The human brain capacity for this meta-organization can be ascribed to evolution of the most recent enlargements that sculpt the temporal and frontal fossae in hominid endocasts. The added cortices should not be conceived of as loci for storage of numerical representations, but as facilitators of global organization of meta-operators.

The eminent neuropsychiatrist and neuropathologist Paul Yakovlev (1962) described human brains as unique in having areas of cerebral cortex without direct connections to and from the basal ganglia. He speculated that these areas might provide the neural insulation from environmental vicissitudes that is necessary for abstract thought. These areas have not to our knowledge been otherwise identified. We postulate that a marker for them might be the lack of identifying cytoarchitecture that characterizes some neocortical areas having so many seemingly identical neurons that their nuclei appear as grains of dust; hence the venerable anatomical term *koniocortex* (Freeman 2009).

Automatic numerical processing is based on an abstract representation

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Abstract: The goal of the present commentary is to show that past results on automatic numerical processing in different notations are consistent with the idea of an abstract numerical representation. This is done by reviewing the relevant studies and giving alternative explanations to the ones proposed in the target article.

As indicated by Cohen Kadosh & Walsh (CK&W), looking at automatic processing provides an informative insight into the nature of the underlying numerical representations that are relatively uncontaminated by task-dependent strategies. Automatic numerical processing was explored in past research using two main paradigms. The first was the size congruency paradigm, showing that automatic numerical processing takes place when participants intentionally compare the physical sizes of numerical stimuli. Of particular relevance are recent works by Cohen Kadosh et al. (2008e) and Ganor-Stern and Tzelgov (2008), which examined automatic processing of numerical magnitude for digits and number words, and for numbers in Arabic and Indian notations. The second paradigm was the SNARC effect, showing automatic magnitude processing and mapping of magnitude to space when participants perform a variety of tasks that do not require magnitude processing. Relevant for the present context are works that looked at the SNARC effect for digits and number words (e.g., Fias et al. 1996; Nuerk et al. 2005).

The target article authors' conclusion from past studies is that the representation underlying automatic processing is notation-specific. This conclusion is mainly based on the fact that the evidence for automatic numerical processing was not identical for the different notations. In this commentary, I suggest that a notation-specific representation does not necessarily follow from the empirical findings, and I propose alternative explanations for the patterns of findings reviewed in detail in the target article.

First, CK&W have cited a series of studies showing more robust evidence for automatic processing of digits than of number words, and have interpreted this pattern of results as supporting the idea of notation-specific representation. It should be noted, however, that automatic processing is heavily influenced by skill level. People are not equally skilled with extracting numerical information from different notations, but rather, they are more skilled in extracting such information from digits than from number words. As a consequence, automatic numerical processing of number words might be more limited than that of digits. Hence, it might take longer time to occur (Cohen Kadosh et al. 2008e), it might not take place when a verbal task is performed (Fias et al. 2001a), or under

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some conditions, it might not occur at all (Ito & Hatta 2003). Thus, it is possible that there is a common underlying abstract representation, but it could be that it takes longer to access it from a number word compared to a digit. In some cases the processing of the relevant dimension is fast enough so that the relatively slow process of accessing the abstract numerical representation from the number word does not interfere with it.

Second, CK&W have based their argument for a notation-specific representation underlying automatic processing on the fact that the size congruency effect took a slightly different form for the different notations (Cohen Kadosh et al. 2008e; Ganor-Stern & Tzelgov 2008). The problem with the argument is that this effect reflects the interaction between the processing of the relevant and irrelevant dimensions, and a difference in this interference effect between notations might stem from the relevant physical size dimension and not from the irrelevant numerical one. Therefore, this should not be seen as evidence for a notation-specific underlying representation. For example, in Dehaene and Akhavein's (1995) study, the absence of a distance effect in the physical same-difference task for pairs composed of a digit and a number word may very well be due to the fact that such pairs are so physically dissimilar – which makes the decision faster and, as a consequence, too short to be affected by the processing of the irrelevant dimension. Indeed, our recent study that used two numerical notations (Arabic and Indian) was able to show evidence for automatic numerical processing when the numbers were presented in different numerical notations (Ganor-Stern & Tzelgov 2008).

The debate over the interpretation of Ganor-Stern and Tzelgov (2008) or Cohen Kadosh et al. (2008e) seems to be a case of which half of the glass you are looking at. In my opinion, the fact that incongruency between numerical and physical sizes affected performance in the physical task, even in mixed-notation pairs, seems to be especially strong evidence for the idea of an abstract representation (Ganor-Stern & Tzelgov 2008). More support is provided by studies reporting a size congruency effect not only for numbers but also for number words (Ansari et al. 2006b; Cohen Kadosh et al. 2008e). CK&W, in contrast, seem to focus on the empty half of the glass and to spotlight the differences in the pattern of results for the different notations. As explained earlier, some of these differences might be a product of other factors and are not informative as to the nature of the underlying numerical representation; and some may even be accidental.

More generally, it seems that the authors set the criterion that *any* non-additive difference between the numerical processing of the different notations is evidence for a notation-specific representation. This criterion might be too lenient, as not all differences are theoretically relevant for the issue in question. As explained earlier, some of the differences are due to skill level, some are due to the nature of the relevant dimension, and some are truly accidental. In the debate over the issue of abstract/non-abstract representation, attention should be given only to such differences that are either theoretically interpretable or at least that are replicable across studies.

Finally, one of the main points made by the target article is the importance of studying automatic processing in addition to intentional processing. Behavioral studies indeed provided evidence for dissociable patterns of results in the two modes of processing (Ganor-Stern et al. 2007; Tzelgov et al. 2009). Unfortunately, brain-imaging studies that looked at intentional and automatic numerical processes did not report such a dissociation in terms of different electrophysiological activity, or areas being active when the two modes of processing were taking place (Ansari et al. 2006b; Cohen Kadosh et al. 2007c). Future neuropsychological research should attempt to dissociate these two types of processes in terms of the underlying brain activation.

Expertise in symbol-referent mapping

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Abstract: Much evidence cited by Cohen Kadosh & Walsh (CK&W) in support of their notation-specific representation hypothesis is based on tasks requiring automatic number processing. Several of these findings can be alternatively explained by differential expertise in mapping numerical symbols onto semantic magnitude representations. The importance of considering symbol-referent mapping expertise in theories on numerical representations is highlighted.

The target article by Cohen Kadosh & Walsh (CK&W) can be considered as very timely in light of increasing evidence suggesting a strong impact of input format on numerical information processing (e.g., Campbell 1994). One explanation for such findings is CK&W's proposal that different neuronal networks represent numerical quantity depending on the notation. The authors do not only distinguish between non-symbolic (e.g., dot patterns) and symbolic formats, but also suggest separate representations for different symbol systems (e.g., Arabic digits vs. number words). In their dual-stage model, they argue that the (initial) automatic processing of numerical information relies on these non-abstract, notation-specific representations, whereas (later) intentional processing could lead to the creation of connections between them and give rise to result patterns congruent with the abstract-representation view. Therefore, a large part of the findings reported in favor of their hypothesis comes from studies requiring automatic number processing, which should be "unaffected by task demands and intentional strategies" (sect. 5, para. 3).

A critical issue that was not considered by CK&W is the role of expertise in processing different numerical notations. This primarily holds true for number symbols, which, in contrast to non-symbolic representations, have an arbitrary relationship to the numerical magnitude to which they refer (Peirce 1955). Over development, we learn to map these cultural symbols onto semantic magnitude information (cf. Ansari 2008) and attain different levels of expertise for different notations. For instance, we are generally more proficient in the numerical processing of Arabic digits compared to number words, since the former are the standard visual notation for quantity processing and calculation. The more expertise we have acquired for a specific type of numerical symbol, the more likely its presentation leads to an automatic activation of the underlying semantic magnitude representation. A similar account was put forward by Campbell and colleagues in their encoding-complex hypothesis: "task-specific retrieval processes will be more efficient when numerical stimuli appear in a familiar, well-practiced format, relative to the retrieval processes activated by an unfamiliar surface form" (Campbell & Epp 2004, p. 231). If differences in symbol-referent mapping expertise are not considered in tasks drawing on automatic number processing, notation-related effects are not conclusive with regard to the question of non-abstract representations. This point should be illustrated by briefly reviewing some behavioral key findings reported in the target article.

CK&W cited two studies in which interactions between notation and automatic number processing were observed in the size-congruity paradigm (Cohen Kadosh et al. 2008e; Ito & Hatta 2004). These studies revealed that numerical information from number words did not interfere with physical size comparison, whereas such an interference emerged for Arabic digits, indicating that "numerical information was not processed automatically" (sect. 6, para. 1). However, if the semantic representation was not automatically accessed by the number words, presumably due to less symbol-referent mapping expertise for verbal numbers, this result cannot be interpreted as evidence for notation-specific representations. Fias and colleagues

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investigated the well-established SNARC effect using Arabic digits (Fias et al. 1996) and verbal numbers (Fias 2001). Automatic number processing was probed by requiring participants to monitor the occurrence of certain phonemes in the numbers; in the intentional number-processing task parity judgments were required. The latter task elicited SNARC effects for both, Arabic digits and number words. In the phoneme-monitoring task, however, a SNARC effect was only observed for Arabic digits, not for number words. A lack of expertise in mapping number words to semantic magnitude representations can again explain the absence of a SNARC effect in the phoneme-monitoring task. Also, the reported results from the priming study by Koechlin et al. (1999) can be interpreted in a similar vein. Participants were presented a prime number before they had to compare a numerical stimulus to a standard. They observed notation-related effects only when the prime number was subliminally presented (for 66 msec). Specifically, a quantity priming effect (i.e., shorter response times in the number comparison task with decreasing numerical distance between prime and target) emerged for Arabic digits but not for verbal numbers. Koechlin and colleagues discussed these findings in terms of notation-specific representations under demanding temporal conditions, which may converge at a later stage of processing. However, it also appears plausible that the number words were not presented long enough to sufficiently activate the underlying semantic quantity representation. Taken together, notation-related differences in symbol-referent mapping expertise, which result in differential activation of the underlying semantic magnitude representation, can explain the reviewed findings without the need for assuming notation-specific representations.

Symbol-referent mapping expertise may also loom large in understanding individual differences in mathematical competence. Recent studies suggest that little expertise or even deficits in processing numerical symbols are related to poor mathematical performance. Rousselle and Noël (2007), for example, reported that children with developmental dyscalculia displayed similar performance as matched controls in a non-symbolic magnitude comparison task, whereas they performed more poorly in the symbolic task version. Holloway and Ansari (2009) investigated typically developing children and found that only the symbolic, but not the non-symbolic, distance effect predicted later mathematical achievement (but see also Halberda et al. 2008).

The point raised in this commentary is compatible with both the abstract and the non-abstract view of numerical representation in the brain. We may learn to map numerical symbols onto a unitary abstract representation (Dehaene et al. 2003), or we may develop separate representations for these symbols as is proposed by CK&W. At present, our knowledge about the neurocognitive processes involved in the acquisition of symbol processing expertise is very limited. Recent neuroimaging studies revealing developmental (e.g., Ansari et al. 2005) and training-related (e.g., Diester & Nieder 2007) activation changes during basic number processing, however, suggest a high degree of plasticity in neuronal networks coding numerical quantity. Whether evidence for abstract or non-abstract representations is found could thus partly depend on the acquired level of expertise in numerical symbol-referent mapping.

Abstract after all? Abstraction through inhibition in children and adults

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Abstract: I challenge two points in Cohen Kadosh & Walsh's (CK & W) argument: First, the definition of abstraction is too restricted; second, the distinction between representations and operations is too clear-cut. For example, taking Jean Piaget's "conservation of number task," I propose that another way to avoid orthodoxy in the field of numerical cognition is to consider inhibition as an alternative idea of abstraction.

I wish to challenge two points in Cohen Kadosh & Walsh's (CK&W) argument: First, the definition of abstraction is too restricted; second, the authors' distinction between representations and operations is too clear-cut. I challenge their argument from the viewpoint of cognitive developmental psychology, using a famous experimental design by Jean Piaget as an example: the "conservation of number task" (Piaget 1952; 1984).

CK&W discuss the abstraction of number representations only in relationship to the form of the input in which the numerical information was presented; namely, specific verbal or nonverbal means of denoting numbers (following Dehaene's definition). In doing so, they miss directly discussing the question of cognitive abstraction of number representations in relation to space per se. However, numbers in the human brain – particularly in the parietal lobes – also must be abstracted from space. This question is especially relevant in developmental studies on number conservation. Remember that, in the conservation-of-number task (Piaget 1952; 1984), when shown two rows containing the same number of objects, but of different lengths (after the objects in one of the rows have been spread apart), the child has to determine whether the two rows have the same number of objects. Up to the age of 7 years, children erroneously respond that there are more objects in the longer row, reflecting the use of the misleading visuospatial "length-equals-number" strategy that they fail to inhibit (Houdé 1997; 2000; Houdé & Guichart 2001). Moreover, adult brains don't fully overcome this spatial bias; hence, they require an executive prefrontal network to overcome it (Daurignac et al. 2006; Leroux et al. 2006; 2009).

Even if, as stated by CK&W, number representations are primarily non-abstract and are supported by different neuronal populations residing in the parietal cortex, the activation of number representations may nevertheless require that individuals inhibit irrelevant visuospatial cues. In my mind, this executive process corresponds to an abstraction process from space (or perception of space) to numbers. The authors suggest, however, that such intentional prefrontal processes (executive functions, cognitive control, selective attention, and so on) are "important for some numerical *operations*, but not representations" (sect. 9, para. 1, emphasis theirs). I disagree. During cognitive development (Houdé 2000), as well as in the dynamic large-scale-network cognition which characterizes adult brains (Fuster 2003), logico-mathematical operations and representations are not so easily dissociable. The Piagetian concept of number conservation is a good example. It is both a numerical operation *and* a numerical representation, that is, the child's or adult's ability to represent or "keep in mind" (conserve) numbers independently of any irrelevant visuospatial cues (e.g., the unequal lengths of the two rows in Piaget's task). This number representation requires "at its heart" an inhibitory operation. Brain imaging (fMRI) results from our laboratory have clearly shown that this number-conservation ability is sustained, both by posterior (especially the bilateral intraparietal sulcus [IPS] and superior parietal gyrus), anterior-cingulate-cortex (ACC), and prefrontal activations (Leroux et al. 2009).

Other examples of this kind of abstraction process are available in the literature on the neural foundations of logical and mathematical cognition (Houdé & Tzourio-Mazoyer 2003). In the field of deductive reasoning, it has been shown that, after error-inhibition training, a clear activation of the cerebral activation pattern occurred, which shifted from the posterior part of the brain when individuals relied on an erroneous visuospatial strategy to the prefrontal part when they accessed abstract logic (Houdé 2008; Houdé et al. 2000; see also Prado & Noveck 2007).

In conclusion, I think that another way to avoid current orthodoxy in the field of numerical cognition is to consider, beyond the

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question of input notations, an alternative idea of abstraction; that is, abstraction through inhibition in children and adults.

A developmental model of number representation

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Abstract: We delineate a developmental model of number representations. Notably, developmental dyscalculia (DD) is rarely associated with an all-or-none deficit in numerosity processing as would be expected if assuming abstract number representations. Finally, we suggest that the "generalist genes" view might be a plausible – though thus far speculative – explanatory framework for our model of how number representations develop.

Challenging "dogmas" in cognitive neuroscience is important for the advancement of our professional development. Therefore, we highly appreciate Cohen Kadosh & Walsh's (CK&W's) target article, which attempts to challenge the widely held belief that the neural representation of numerosity may be abstract rather than non-abstract. According to "neural constructivism," the representational features of the human neo-cortex are strongly modulated by a dynamic interaction between neural growth mechanisms and environmentally derived neural activity (Quartz & Sejnowski 1997; see also Fisher [2006] for discussion of the gene–environment interdependency). Hence, a closer look at the development of the brain, and in particular, at the development of neural representations of numerosity, will shed further light on the question of whether numbers are represented in an abstract or non-abstract manner.

The primary aim of this commentary is to provide more recent developmental data revealing that number representations in children are not stable, but rather, undergo a developmental shift from distinct (non-abstract) to shared (abstract) representations. Beyond behavioral data, we attempt to apply a functional geneticist view as an explanatory framework for the complex data reported thus far. As outlined rather briefly by CK&W, the findings of the few developmental studies that were dedicated to examining notation-dependent effects on number processing in children largely support the authors' notion that children's number representations are likely to be non-abstract (Holloway & Ansari 2009). Maybe even more interesting is the finding that 3-year-olds' abilities to compare non-symbolic number sets seem to rely on perceptual cues if the ambiguity between (discrete) numerical and (continuous) non-numerical stimulus properties is overwhelming (Rousselle et al. 2004). The latter results clearly speak against the notion of an abstract number representation. A similar conclusion has been drawn by Butterworth (2005), who argues that "if put into conflict . . . continuous quantity seems a more powerful cue" (p. 5; see also Mix et al. 2002). Five-year-old children are able to compare and add large sets of elements presented in different non-symbolic modalities (dot arrays, tone sequences) (Barth et al. 2005). Importantly, the authors' report a significant interaction between the presentation format and the ratio of the two sets to be compared, being characterized by a steeper ratio-dependent decline in cross-modal performance. If one assumes an abstract representation of numbers, no performance differences within and across modalities should have been observed. Likewise, children's mapping between non-symbolic and symbolic number representations becomes more refined with age, which is contrary to expectation if one assumes abstract number representations (Mundy & Gilmore 2009). Findings of dissociations between different notations are not restricted to typically developing children; dyscalculic children also are reported to exhibit impaired performance when comparing symbolic Arabic digits, but not when comparing non-symbolic object sets (Rousselle & Noël 2007).

With respect to developmental dyscalculia (DD) the distinction between automatic and intentional performance is an important one. Empirical evidence, supporting the authors' claim that automatic number processing might be a more powerful tool to assess differential number processing skills, comes from a single-case study of DD (Kaufmann et al. 2004). Results are incompatible with the notion of abstract number representation, as they revealed that number-processing deficiencies predominantly emerged upon automatic, but much less upon intentional number processing. A further interesting issue in this case study was the finding of operation-specific effects in fact retrieval (addition and subtraction facts being relatively preserved, while multiplication facts were severely impaired; Kaufmann 2002). In our view, operation-specific effects (which have been frequently reported in the patient literature, e.g., Pesenti & van der Linden 1994) – like effects of notation – are not in line with an abstract view, but rather, are strongly suggestive of the existence of distinct number representations.

Finally, we suggest that the "generalist genes" theory may provide a plausible – though thus far, speculative – explanatory framework for the view that number representations undergo a gradual developmental change (Kovas & Plomin 2006). In particular, concepts of polygenicity (many genes affect one trait/one cognitive domain) and pleiotropy (one gene affects many traits/cognitive domains) are not only apt to explain the frequently observed comorbidity between DD and other learning disabilities such as dyslexia or attention disorders, but may also provide a useful theoretical framework for the assumption that number representations become shared (abstract) with more experience/practice, which is inevitably accompanied by a more fine-tuned gene–environment interdependency (Fisher 2006; Kovas & Plomin 2006).

In sum, developmental findings challenge the existence of an abstract number representation. However, in our view, notation-specific effects are not necessarily indicative for the existence of non-abstract number representations, especially when it comes to developmental studies. The observed interactions between different input modalities could also be a result of deficient mapping between symbolic and non-symbolic representations in children with and without DD. We assume that developmental progress goes along with higher overlap of brain activation between, as well as across, different numerical input modalities. Previously, we found no activation differences between approximate and exact calculation in school children (Kucian et al. 2008). These results, rather, point to a mutual neuronal network for both tasks. However, one has to keep in mind that both tasks have been presented symbolically, differing solely in demands.

Taken together, we suggest that brain activation patterns for different numerical tasks are partly overlapping and that some brain regions are dependent on notation/input modality. Moreover, activation patterns get influenced by task demands such as automatic or intentional number processing. If a core region for number processing exists, it is plausible that this region consists of highly interconnected neurons for different numerical inputs and that activation of one neuronal population quickly spreads to other populations, leading to cross-notational activation, as proposed by CK&W. With development and higher numerical proficiency, these cross-notational activations might increase, reflecting automatization processes. There is probably a gradual difference in definition between non-abstract and abstract representation of numerosity with respect to both the strength of connections and to coactivations of different neuronal

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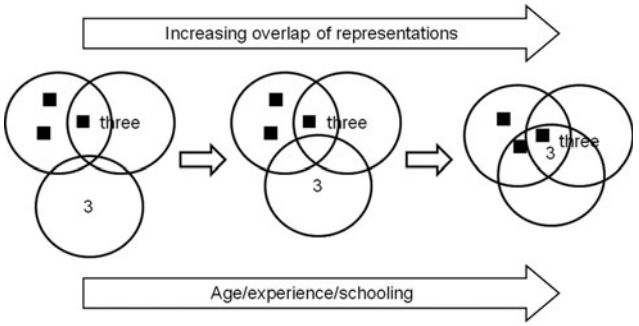


Figure 1 (Kucian & Kaufmann). Our developmental model of number representation proposes an increased overlap of representations across different number notations with advanced expertise, and, furthermore, implies a gradual shifting from non-abstract to abstract representations of numerosity.

populations. If, for instance, the connection is extremely tight and both neuronal populations get activated simultaneously independent of inputs, one could label it as an abstract numerical representation, although this representation is built up by distinct neuronal populations. Upon summarizing the above-mentioned findings, we propose the following developmental model (Fig. 1) of how number representations might be formed:

Symbols in numbers: From numerals to magnitude information

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Abstract: A dual-code model of number processing needs to take into account the difference between a number symbol and its meaning. The transition of automatic non-abstract number representations into intentional abstract representations could be conceptualized as a translation of perceptual asemantic representations of numerals into semantic representations of the associated magnitude information. The controversy about the nature of number representations should be thus related to theories on embodied grounding of symbols.

The review of Cohen Kadosh & Walsh (CK&W) in the target article demonstrates that numerical representations are modulated by task demands. The authors propose the existence of two cognitive codes for numbers, that is, (1) an automatic non-abstract representation, which is notation and modality dependent, and (2) an intentional abstract representation, which is notation and modality independent. We agree with this hypothesis. However, we think that a dual-code model of number representation needs to take into account further aspects about the differences in the nature of the two representations and should theoretically distinguish between an asemantic representation of the symbolic stimulus (e.g., Arabic numeral) and the representation of its associated meaning (e.g., magnitude information). The controversy about abstract magnitude representation in the parietal lobes relates, therefore, directly to the ongoing debate about symbol grounding.

Interestingly, CK&W's model of number processing seems to be inspired by the recently suggested Language and Situated Simulation (LASS) theory of Barsalou et al. (2008) and their proposal of dual codes in embodied representations of conceptual knowledge. Indeed, both models hold that automatic and intentional stimulus processing results in different types of cognitive representations and assume that a deeper deliberate processing is central to the semantic representation of abstract concepts. We believe that both notions provide an interesting framework that contributes directly to the question of whether magnitude representations are abstract or non-abstract. However, we want to point out some substantial theoretical differences between the current model of number processing and dual-code models on conceptual knowledge in psycholinguistic research.

First, most dual-code models of semantic processing view the faster emerging automatic representation as an asemantic stimulus coding that does not go beyond a perceptual, linguistic, or phonological representation of the presented word or number symbol (see, e.g., Barsalou et al. 2008; Mahon & Caramazza 2008). The target article shows that effects of magnitude processing are modulated by the notation of the number symbol if and only if the task does not require any semantic processing of the numerical magnitude information. Taking a closer look at studies on automatic processing that provide evidence in favor of non-abstract number representations, it becomes clear that effects of number meaning are smaller or even nonexistent if the number stimulus is perceptually more complex (e.g., number words vs. digits: Cohen Kadosh 2008a; or Japanese Kanji numbers vs. Kana numbers: Ito & Hata 2003) or printed in an unfamiliar notation (e.g., Indian vs. Arabic digits: Ganor-Stern & Tzelgov 2008). Moreover, CK&W argue that because automatic processing is unaffected by intentional strategies, indirect number tasks provide an unbiased inside look into the nature of the representation of numerical magnitude information. However, an alternative reason for the presence of notation-dependent effects in these tasks might be that automatic processing of number words and unfamiliar symbols is likely to be restricted to a superficial stimulus coding without activation of the underlying numerical magnitude information. We consequently assume, in line with dual-code models of conceptual knowledge (Barsalou et al. 2008), that under conditions of automatic processing, complex and unfamiliar number symbols will be merely transcoded and represented asemantically in a perceptual, linguistic, or phonological format. It is therefore questionable whether the automatic non-abstract number representation proposed by CK&W can be understood as a semantic representation of numerical magnitude information. Alternatively, the transition from an automatic to an intentional numerical representation might be better conceptualized by different levels of semantic processing and the translation of a perceptual representation of the number symbol into a semantic representation of the associated magnitude.

Second, a central aspect of the LASS theory of Barsalou et al. (2008) is the assumption that abstract symbols such as words and numbers become meaningful only when they are somehow mapped to concrete bodily experiences (the so-called embodied cognition hypothesis; for reviews see, e.g., Fischer & Zwaan 2008). Following this view, intentional number processing consists of an activation of correlated information in brain areas that originally evolved to process non-symbolic stimuli, that is, perceptual and motor areas. This embodied mechanism of conceptual knowledge representation has been described as perceptual and motor resonance (Rueschemeyer et al., in press a) and represents a bidirectional coupling of semantic representations with processes of action planning and motor control. Interestingly, empirical evidence for such a sensorimotor grounding of symbol meaning has not only been reported by studies on word processing (Glenberg & Kaschak 2002; Lindemann et al. 2006; Rueschemeyer et al., in press b; Zwaan & Taylor 2006), but has also been recently shown for the processing of Arabic digits in numerical tasks (Andres et al. 2004; Fischer 2008; Lindemann et al. 2007). One might therefore speculate that the abstraction

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of number meaning consists of an association between the numerical information and magnitude-related motor codes – an assumption that is in line with the idea that magnitude representations for numbers and actions share common cognitive codes within a generalized system for size and quantity (Walsh 2003).

Since the notion of embodied cognition is one of the most controversially debated hypotheses of recent psycholinguistic dual-code models of conceptual processing, the principle of motor resonance should also be addressed in the context of number processing models. In conclusion, we think that the idea of an action-based number semantics might provide new insights into the nature of numerical magnitude representations, and might thereby fruitfully contribute to future theoretical developments in mathematical cognition research.

Inactivation and adaptation of number neurons

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Abstract: Single-neuron recordings may help resolve the issue of abstract number representation in the parietal lobes. Two manipulations in particular – reversible inactivation and adaptation of apparent numerosity – could provide important insights into the causal influence of "numeron" activity. Taken together, these tests can significantly advance our understanding of number processing in the brain.

Cohen Kadosh & Walsh (CK&W) present a comprehensive argument against the abstract representation of numbers in the parietal lobes. Their discussion focuses on behavioral and neuroimaging studies, which comprise the bulk of the numerosity literature. But, as CK&W point out, these techniques do not provide the sampling resolution necessary to definitively answer the question of abstract number representation. In contrast, single-neuron electrophysiology provides high spatial and temporal resolution, allowing researchers to monitor the activity of individual neurons in real time. This technique is therefore the most promising avenue for addressing the issue of abstract number representation. In this commentary, I present two single-neuron experimental manipulations that, to my knowledge, have not been used in studies of number-sensitive neurons. These manipulations could help move single-cell studies beyond simple correlation to a more causal understanding of the neuronal basis of number processing.

First, temporary pharmaceutical inactivation (Li et al. 1999; Wardak et al. 2002) of number-sensitive patches of parietal cortex can be used to test the usefulness of reported number representations. Although it would be a challenge to demonstrate that all number neurons were inactivated in the parietal lobe, a large portion of neurons can be reliably "switched off" and reactivated over time. Accordingly, animals should show severely diminished performance on number-related tasks during inactivation if numerons truly support their ability to accurately process numerosity. Following the lead of the tasks reviewed in the target article, number-related task performance would have to be assessed across different number formats. The existence of abstract number representations predicts comparable decreases in performance regardless of number format when compared to pre-inactivation measurements. Temporary inactivation is therefore one way in which our understanding of number representations can progress beyond correlational evidence.

If abstract number neurons exist, then they presumably underlie our ability to perceive and process various numbers. Thus, to tease apart the influence of number neurons on perception, it would be useful to have a situation in which perceived numerosity can be manipulated independently of displayed numerosity. Fortunately, such a psychophysical "trick" has been recently discovered (Burr & Ross 2008; see also Durgin 2008).

The second manipulation involves the "apparent numerosity adaptation" paradigm (Burr & Ross 2008). In this task, subjects fixate a center target while two patches consisting of many stationary stimuli are presented, one to the left and one to the right of fixation. Immediately after an extended period of adaptation, test patches are then presented in the same two locations and subjects are asked to make a numerical judgment, usually in the form of a two-alternative forced choice task (e.g., "Which patch contains more items, left or right?"). Burr and Ross (2008) showed that adapting to a large number of stimuli decreases subsequent numerosity judgments, while adapting to a small number of stimuli produces artificially increased numerosity judgments. The numerical perception of the subjects can therefore be manipulated in a controlled manner based on the number of stimuli in the adapting patch.

For single-neuron recordings, this task could be passively presented to animal subjects. Better yet, animals could be trained to make "more" or "less" judgments when the two test patches are presented after adaptation. We can then ask how number neurons in parietal cortex respond over time in the adaptation task (i.e., during and after adaptation). For example, if a neuron with a preferred numerosity of 20 (Nieder & Merten 2007) is isolated and the animal is adapted with a patch of 100 stimuli, will the subsequent test presentation of 20 stimuli cause the neuron to fire maximally, consistent with the veridical presented number? Or, alternatively, will the neuron's response shift towards the adapted numerosity, in line with the subject's percept? Again, different formats of number stimuli can also be used for adaptation and testing (Diester & Nieder, in press). Following the labeled-line coding hypothesis (Nieder & Merten 2007), numeron selectivity should be predictably manipulated by low- and high-numerosity adaptation across formats. A series of systematic adaptation-and-test conditions on the same neuron would help elucidate the functional role of number neurons, and shed light on the issues of automaticity and intentionality raised by CK&W.

A combination of the two manipulations may prove to be the most fruitful. Changes in task performance during inactivation – both in the standard delayed-match-to-sample task (typically used by Nieder and colleagues) and the adaptation task proposed above – can be used to assess the function of number neurons in numerosity judgments. This investigation could be extended to putative number-sensitive neurons in prefrontal cortex (PFC). This extension would help disambiguate the role of parietal and prefrontal number neurons, as well as allow for the testing of CK&W's hypothesis that PFC plays a "post-representational" role in relation to number processing in the parietal lobes.

These two manipulations are, to be sure, not complete experiments. But they are based on established techniques in the field that are well within our current capabilities. The onus to carry out these experiments is on proponents of abstract number representation because, as CK&W highlight, there are currently too many issues of interpretation to conclude in favor of abstractness. Regardless, for both sides of the issue, a straightforward manipulation of the responses of single neurons seems to be the most definitive method for uncovering the abstractness of number representations in the parietal lobes.

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Non-abstractness as mental simulation in the representation of number

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Abstract: Abstraction is instrumental for our understanding of how numbers are cognitively represented. We propose that the notion of abstraction becomes testable from within the framework of simulated cognition. We describe mental simulation as embodied, grounded, and situated cognition, and report evidence for number representation at each of these levels of abstraction.

Whether the human mind computes numerical information by creating uniform abstract representations of magnitude or by making reference to distinct modality- and notation-specific representations is an important theoretical question. Similarly to Cohen Kadosh & Walsh (CK&W), we favor the latter view, but we also propose the notion of "simulation" to further clarify the quality of such representations. Ambiguity in defining "abstractness" leads to attribution of several features (e.g., automaticity, implicitness/explicitness, and generalizing power) to number representations without explaining how they are related hierarchically and functionally. Without this elaboration, specific predictions and implications for non-abstract theories of numerical cognition may also remain ambiguous.

The *simulation* theory of cognition (e.g., Barsalou et al. 2008) avoids such ambiguities. Simulation in this view is "the re-enactment of perceptual, motor and introspective states acquired during experience with the world, body and mind" (Barsalou 2008, p. 618). We agree with the idea that simulation is the principle diagnostic feature of non-abstractness and propose a further distinction between *grounded*, *embodied*, and *situated* conceptual simulations. The resulting hierarchy helps to clarify the empirically testable implications of this view for human cognition in general and explain the wide range of features specific to numerical representations. In the following, we first describe this hierarchy and then provide empirical support.

A cognitive representation is grounded when its structure reflects the properties of the Euclidean world. This is the most fundamental aspect of non-abstract representations. Next, a cognitive representation can be embodied if it is bound by the experiential (e.g., perceptual or motor) constraints imposed by the human organism. Not all cognitive representations are embodied (e.g., some dreams). Finally, a cognitive representation can be situated when it is sensitive to the context in which it is generated.

The experimental study of number processing provides ample evidence for a simulation view of numerical cognition. Specifically, we think that the spatial biases known to accompany number processing (SNARC effect; see Figure 1 of the target article) systematically highlight the features of non-abstract number representation. Grounding, for example, is revealed in the association of larger numbers with upward positions and smaller numbers with downward positions (Schwarz & Keus 2004; see also Fischer & Campens 2008). The embodiment of number processing is evident from effects of finger counting habits on adult number processing (Fischer 2008) and from the spontaneous modulation of grasp aperture by task-irrelevant number magnitudes (Andres et al. 2008). Finally, situatedness

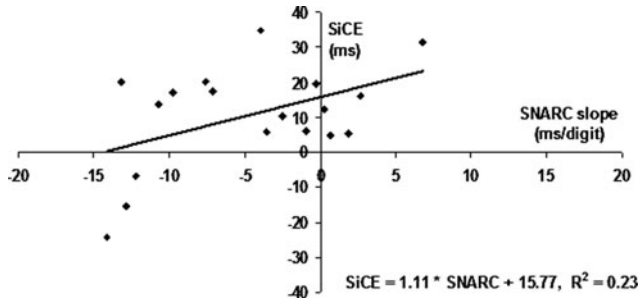


Figure 1 (Myachykov et al.). Participants with a typical SNARC (left side of the graph) tend to have a weaker size congruity effect (SiCE). This suggests a conflict between attention to physical and semantic aspects of numbers.

of numerical cognition is indicated by the range-dependence of the SNARC effect that shows that we take into account (or simulate) the current relative meaning of numbers (see Fischer 2006, for evidence and discussion). CK&W correctly point out that such context-dependence is especially evident in the cognitive representation of negative numbers (Fischer 2003; Fischer & Rottmann 2005). Understanding non-abstract representations as cognitive simulations along the dimensions of grounding, embodiment, and situatedness provides a theoretical platform for real-life number representation. The proposed hierarchy of features of number representation allows us to interpret observed effects within an interconnected model.

A recent study of both SNARC and size congruity effect (SiCE; see sect. 6 of the target article) illustrates how features of non-abstract number representation interact. In a speeded binary classification task, 18 participants indicated whether single digits were more or less than 5. Digits 1, 4, 6, and 9 were randomly shown in either 12- or 60-point font size. In addition to the typical SNARC ($p < .01$) and SiCE ($p < .01$) effects, we found a positive correlation between the two ($p < .05$; see our Fig. 1): Participants with a strong SiCE tend to have a weaker SNARC. This interaction between SiCE and SNARC indicates that features of number representation compete for the same cognitive resource. One possible interpretation of this novel result from the perspective of cognitive simulation theory is that attending to irrelevant physical attributes of digits grounds their cognitive representation. This may, in turn, prevent their embodiment by inhibiting their mapping onto space. Further studies of the task-dependence of number simulation will clarify to which extent SiCE and SNARC can be situated (Platenburg et al., in preparation).

A re-analysis of recently published data supports the view that number representations can be simulated on-line. In a pointing task (Pinhas & Fischer 2008), adults located the results of addition or subtraction problems on a visually presented line with flankers 0 and 10 on a touch screen. They located the same number more rightward during addition (e.g., $4 + 2$) than during subtraction (e.g., $8 - 2$). This suggests a simulation of addition as rightward movement along a mental number line and a simulation of subtraction as leftward movement. A congruency effect in pointing times supports this interpretation and shows that our task evoked grounded, embodied, and even situated number representations. We next tested the prediction of CK&W's processing model that non-abstract effects are more prevalent for fast compared to slow responses. To do this, we split each participant's response times in the zero problems (e.g., $4 + 0$, $4 - 0$) along the mean of their distribution into fast and slow responses. The spatial simulation effect was significant for fast responses, $t(13) = 2.66$, $p < .02$, but not for slow responses, $t(13) = 1.65$, $p > .12$. This result supports CK&W's proposal (see their Fig. 5) that automatic number processing precedes intentional processing. It is worth noting that this outcome

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is actually *in conflict* with Barsalou et al.'s (2008) suggestion that situated simulations always follow abstract (language-based) representations.

Numbers and numerosities: Absence of abstract neural realization doesn't mean non-abstraction

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Abstract: The neural realization of number in abstract form is implausible, but from this it doesn't follow that numbers are not abstract. Clear definitions of abstraction are needed so they can be applied homogenously to numerical and non-numerical cognition. To achieve a better understanding of the neural substrate of abstraction, productive cognition – not just comprehension and perception – must be investigated.

Cohen Kadosh & Walsh (CK&W) provide a compelling argument for challenging the currently accepted view – intuitively appealing and convenient – that the nature of numerical representation is inherently abstract. They lucidly explain why it is implausible that number has a single specific representation center given that classic cases for external world attributes such as color and motion lack a single locus of representation. In reviewing relevant behavioral, neuroimaging, and single-neuron (monkey) studies, they convincingly show that, despite the fact that many reports appear to support the abstract representation view, the evidence is incomplete and presents serious methodological and theoretical problems (e.g., null results, paradigm insensitivity, task specificity factors). Indeed, the data seem to support the opposite view. However, contrary to what the authors' defend, from this it doesn't follow that "numbers are not abstract" (sect. 5's title). The authors' definition and usage of crucial concepts such as "abstraction," "representation," and "number," lacks conceptual clarity and creates unnecessary confusion and discontinuities with the understanding of other realms of cognition. Here, I only address the first one – abstraction.

CK&W provide a narrow and confusing characterization of abstraction. First, they adopt a behavioral definition (sect. 2, para. 1) that applies exclusively to numbers (and, as an extension, they operationalize the notion of abstract representation in terms of neuronal populations' insensitiveness to the form and notation of the input in which numerical information is presented). This operational definition of abstraction is specific but unnecessarily restrictive, making its extension to other non-numerical areas of cognition hard, if not impossible. How are we to relate the authors' arguments with other, presumably supra-modal conceptual domains? Second, the authors' terms "abstract" and "non-abstract" as defined in the narrow domain of neural sensitiveness, become unfortunate misnomers that generate confusion. The only hint the authors give of the nature of (not specifically numerical) abstraction, is a reference to Barsalou (sect. 10, para. 1): "abstraction is a skill that supports goal achievement in particular situations" (Barsalou 2003, p. 1184). But, this is vague and incomplete. That work deals with concepts that refer to entities or state of affairs "about the world" (e.g., chair), where even the abstract concept of *truth* is analyzed in that manner (p. 1185). What can then be said about the passage from the abstracted cardinal numbers to, say, transfinite or infinitesimal numbers (i.e., actual infinity), cases in which there is no fact about the world that corresponds to the concept (Núñez 2006; in press; Lakoff & Núñez 2000)? We do need the term "abstraction" in order to correctly handle such concepts. And we do need the authors' arguments to clearly address the fact that neuronal populations are sensitive to form of input. What is required is a fruitful theoretical proposal of supra-modal entity processing (e.g., numbers) that is able to encompass the authors' arguments while leaving room for fruitful distinctions between abstract and non-abstract concepts in a way that is clearly extendable, without discontinuities, to other forms of everyday and mathematical abstraction.

In addressing abstraction, CK&W make a distinction between automatic and intentional processing (of numerical information with different notations). By automatic, they mean a process that does not need monitoring to be executed (sect. 5, para. 3). They argue that by adopting such a distinction, we can yield a better characterization of abstract and non-abstract representations (sect. 11, para. 4). And they go on to build a parallel between this distinction and Barsalou's linguistic and situated simulation (imagery) systems. But, again, this is narrow and problematic. The authors' arguments are mainly concerned with the side of cognition that deals with perception and comprehension. When we look at the productive side of cognition we can see that the automatic/intentional (and linguistic/imagery) distinction can be really troublesome. Consider a person who, during an everyday conversation, says, "that was way back in my childhood," and while doing so points with her thumb backwards over the shoulder. Such speech-gesture coproduction (1) is not monitored (McNeill 1992) and, therefore, is "automatic," and (2) it is inherently abstract because the uttered word "back" and the backwards pointing don't refer to anything in the real world, but to the past, which is metaphorically conceived as being spatially behind ego (Núñez 1999; Núñez & Sweetser 2006). Moreover, this fast spontaneous speech-gesture coproduction is, both, linguistic *and* imagery-driven. When trying to understand the productive side of cognition involving abstract concepts (numbers included) and their neural instantiations, the authors' distinctions break down. More conceptual clarity is needed.

But, looking at the productive side of cognition can actually be quite supportive of the CK&W's claims. For instance, the authors argue that "it is entirely possible that similar behavioural effects can be subserved by different areas, or neuronal populations in a single brain area" (sect. 5, para. 1). Regarding our space-time mapping example, it is known that humans can spontaneously conceptualize temporal events as being spatial locations along the sagittal axis, with events in the future as being in front of ego and events in the past as being behind. And, neurally, this can be instantiated through the recruitment of neural populations in the ventral intra-parietal area (VIP) and the polysensory zone (PZ), among others (Núñez et al. 2007). However, the linguistic and spontaneous gestural production of the Aymara of the Andes shows a striking counterexample: They conceive future events as being behind them and past events as being in front of them (Núñez & Sweetser 2006; AAAS 2006). These two forms of spatial conceptions of time are internally consistent but mutually inconsistent, having, presumably, different neural realization. Similarly, numbers and arithmetic can be realized conceptually through different metaphorical mappings such as object collection and motion along a path (Lakoff & Núñez 2000). These distinct mappings can have different neural instantiations while supporting the same inferential organization (e.g., in both cases "two plus three is five.") Both conceptions characterize a cascade of isomorphic entailments, which are presumably, as the authors claim, subserved by different neural populations in the brain.

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The discussion of methodological limitations in number representation studies is incomplete

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Abstract: Cohen Kadosh & Walsh (CK&W) discuss the limitations of the behavioral, imaging, and single-cell studies related to number representation in human parietal cortex. The limitations of the imaging studies are grossly underestimated, particularly those using adaptation paradigms, and the problem of establishing a link between single-cell studies and imaging is not even addressed. Monkey functional magnetic resonance imaging (fMRI), however, provides a solution to these problems.

Cohen Kadosh & Walsh (CK&W) correctly point out that assessing technical limitations is critical in weighing the evidence favoring one or the other of the opposing views, abstract or non-abstract, about numerical representation in parietal cortex (PC). On at least three counts, they have overlooked relevant limitations.

CK&W state that: "Single-cell neurophysiology offers better temporal and spatial resolution than human neuroimaging" (sect. 8, para. 1). While strictly true, this seems to imply that the two techniques are measuring the same variable. This is of course untrue: The functional magnetic resonance imaging (fMRI) measures a haemodynamic response, not neuronal activity. Contrary to what has been conveniently assumed, the relationship between these two variables is far from resolved and depends upon the experimental conditions: while the link might be relatively direct in passive sensory stimulation, this is not the case when using task paradigms (Sirotin & Das 2009). The statement also ignores the whole issue of homology between the human and monkey brain, which we have only begun to resolve with the advent of monkey fMRI (Orban et al. 2004). Two facts are particularly relevant here. The surface area of the cortical sheet is ten times larger in humans than in the monkey (Van Essen 2004), which implies that human cortex includes two to five times more functional areas than its monkey counterpart. On the other hand, the relationship of these areas with cortical sulci having identical labels can differ between the species, as the human MT/V5 complex illustrates. In human parietal cortex, the regions corresponding to the lateral bank of monkey intraparietal sulcus (IPS) are located in the medial bank of human IPS, especially on the posterior side (Grefkes & Fink 2005). This implies that the homologue of monkey ventral intraparietal (VIP) area, where Nieder records his numerically selective neurons (Diester & Nieder 2007), is not actually located in the human IPS!

CK&W present the results of fMRI adaptation experiments as one of the main indications for a non-abstract representation in PC. They neglect the evidence that adaptation differs between time scales and between cortical areas (Krekelberg et al. 2006; Verhoef et al. 2008). More seriously, they failed to see the implications of the Sawamura et al. (2006) study, which they did quote in their review. Briefly, Sawamura et al. showed that inferotemporal (IT) neurons which respond equally well to two stimuli, say, images of a pig and of a hammer, will adapt when the two identical images follow one another, either two pigs or two hammers, but not, or much less, when the hammer follows the pig or the reverse. Thus, adaptation overestimates neuronal response selectivity and functional magnetic resonance adaptation (fMRA) cannot be used to derive neuronal tuning widths, as in Piazza et al. (2004). The results also imply that at these high levels adaptation occurs not at the cell soma level, but somewhere earlier, either in the dendritic tree or in the inputs. The use of adaptation to prove a non-abstract representation actually implies adaptation at the soma. If this assumption does not hold, the predictions for the abstract and non-abstract case become identical. Exactly the same argument can be made for the combination of adaptation with transcranial magnetic stimulation (TMS), presented by CK&W as their second main argument for non-abstract representation. If adaptation does not involve the cell soma, both hypotheses predict that the parietal neurons will be equally active, and hence, that TMS will have the same effect, opposite to what has been assumed. This dramatic example shows that it is of utmost importance that assumptions made in interpreting fMRI data, be tested. This also holds for the multivoxel technique.

The final evidence for non-abstract representation are the Nieder single-cell data (Diester & Nieder 2007), but here CK&W neglect the limitations that the experimental model imposes upon these results. To be sure, the monkey is the best model that we have experimental access to, but it is not perfect, as there is ample evidence for differences in brain size (Van Essen 2004) and cognitive competences (Penn et al. 2008) between the two species. Hence, what applies to the monkey may not necessarily hold for the human. It is conceivable that the non-abstract representation in the monkey is supplemented in humans by abstract representations, say, in the evolutionarily new areas of the parietal cortex.

Does this mean, then, that the evidence for an abstract representation is solid? This is not the case either. As CK&W correctly pointed out, even it had been demonstrated that different numerical notations activated the same voxels in PC, this need not imply that the representation is carried by a single neuronal population. It is important to notice that even this demonstration is unconvincing thus far, given the extensive smoothing and averaging across subjects that is typical of most fMRI studies (Georgieva et al. 2009).

Unfortunately, the authors in their discussions of future directions completely overlooked the studies that provide a solution to the problems outlined here: fMRI in the awake monkey (Vanduffel et al. 2001). In fact, it replaces a direct comparison between human fMRI and single-cell studies in monkeys, which involves two unknowns, with two comparisons, each of which involves only a single unknown that can be resolved (Orban 2002). The comparison between single-cells and MR signals in the monkey allows one not only to address the relationship between neuronal activity and MR signals (Logothetis et al. 2001; Sirotin & Das 2009), but equally important, to understand the relationship between MR procedure and neuronal selectivity. This procedure can take a variety of forms: it may be a slow adaptation procedure (Nelissen et al. 2006), or a test, based on a comparison of response levels under different conditions (Georgieva et al. 2009). On the other hand, a comparison of fMRI in humans and monkeys allows the homology question to be addressed, when multiple properties of several neighboring regions are compared (Durand et al. 2009). The integration of single-cell studies and human functional imaging using awake monkey fMRI creates a brilliant future for cognitive neuroscience and lies at the heart of translational research in cognitive neurology.

Abstract or not abstract? Well, it depends . . .

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Abstract: The target article by Cohen Kadosh & Walsh (CK&W) raises questions as to the precise nature of the notion of abstractness that is intended. We note that there are various uses of the term, and also

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more generally in mathematics, and suggest that abstractness is not an all-or-nothing property as the authors suggest. An alternative possibility raised by the analysis of numerical representation into automatic and intentional codes is suggested.

We support Cohen Kadosh & Walsh's (CK&W) well-argued warning against sliding into the dogma of assuming a uniform abstract representation of number in the intraparietal sulcus, regardless of modality of input or purpose of the task. This question is especially pertinent now, given the last three decades of research into visual reasoning in mathematics and the recent application of work in embodied cognition to mathematics representation and reasoning. Our interest is from a cognitive science and philosophical, as opposed to a neuroscientific, perspective.

In general, we find the notion of abstraction in the field to be not well-defined. In the article, we are given an initial operational definition from Dehaene, where the presence of an abstract representation, the "behavior depends only on the size of the numbers involved, not on the specific verbal or non-verbal means of denoting them" (Dehaene et al. 1998a, p. 356). But towards the end of the article (sect. 10, para. 1), CK&W cite approvingly Barsalou's comment that "abstraction is simply a skill that supports goal achievement" (Barsalou 2003, p. 1184). Is this in fact consistent with the earlier operational definition? Barsalou's own characterisations in Barsalou (2005) of the use of the term *abstract* include a sense in which perception is in itself typically abstract, inasmuch as it involves categorical judgements out of the "confusion of experience." As this addresses the central issue of the target article, a clearer account of what is at stake here is required.

We do not think that the binary distinction between abstract and not abstract is the right way to conceptualise the problem. In identifying the digit 2 over a range of typefaces, or ignoring the colour of a number of dots in the visual field, it is natural to consider that there is abstraction from the token that is physically present. Certainly the mathematical notion of abstraction allows many levels of abstraction, and we believe that mathematical cognition in general is built in part on some version of arithmetical representations. (This notion of abstraction is also referred to in Barsalou [2005], allowing that there is a question of the degree of abstractness in this case.)

CK&W's analysis in terms of automatic and intentional codes is clearer, and seems potentially of greater explanatory power than deciding on the question of abstractness. Here we note the comments on this topic in Wilson (2002), on the apparent paradox that in more elaborate tasks, the more automated approach actually allows finer control of the activity than do more "controlled" strategies. The suggestion is that the automation builds up internal representations, thereby providing a more efficient way to deal with some of the regularities of the problem at hand. Thus, with practice in arithmetical calculation, more persistent representations will be formed, and on this view these may well be more abstract.

The distinction between automatic and intentional processing raises the question of how automatic compares to the so-called *innate arithmetic* of Lakoff and Núñez (2000). A series of screen experiments on babies (not mentioned by CK&W) suggest that babies are born with basic addition and subtraction skills on small numbers, and indeed appear to recognise sameness of number when objects are replaced with an identical number of different objects (Simon et al. 1995). Presumably, the processing here is automatic, but we are curious as to how these results fit with the authors' account of numerical representation.

Lakoff and Núñez (2000) emphasise the metaphorical process in mathematical development. They identify four "grounding metaphors" for arithmetic (metaphors in which the source domain is a familiar, environmentally grounded domain) that all abstract into a common target domain. These metaphors are all principally visual. The sense of abstraction here is close to the sense in which the term is used in informatics generally, where structure common to some data or mathematical entities can be reasoned about while ignoring properties that differ from instance to instance. Similarly, multi-modal representations of mathematics such as diagrammatic or algebraic reasoning are assumed to abstract to a common domain. It may therefore be relevant to consider work on the cognitive status of metaphor processes.

In Lakoff (2008), it is claimed that mirror neurons are multimodal, that is, the same mirror neurons fire whether we imagine, or perform/perceive certain actions. The neural theory is based on the premise that if we see two domains simultaneously enough times, then connections between the nodes that process the domains are strengthened and we build a strong association. It is not clear to us if there is substantial disagreement between Lakoff's views, as applied to arithmetic, and the views of CK&W. The target article naturally does not address the issue, of interest to us, of how arithmetical judgements that quantify over all numbers are represented (e.g., associativity of addition). This can be expected to relate to the representation of particular numbers, but remains, as far as we know, an open question.

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Common mistakes about numerical representations

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Abstract: Cohen Kadosh & Walsh (CK&W) argue that recent findings challenge the hypothesis of abstract numerical representations. Here we show that because, like many other authors in the field, they rely on inaccurate definitions of abstract and non-abstract representations, CK&W fail to provide compelling evidence against the abstract view.

Whereas number magnitude was initially assumed to be represented abstractly as a function of powers of ten (McCloskey et al. 1985), an analog representation figuring numerical magnitudes by overlapping activations on an oriented and compressed mental line was later proposed (Dehaene 1992). These views have often been mixed ill-advisedly, and it is now common to read that the parietal cortex hosts "an abstract numerical representation taking the form of an oriented number line" (e.g., Cohen Kadosh et al. 2005; Dehaene et al. 1998a). This, however, is a double nonsense: by definition, analog representations cannot be abstract; by essence, abstract representations cannot be oriented or compressed. This conceptual drift from an analog to an abstract number line occurred because many authors in the field used loose definitions of abstract/analog representations leading to several profound mistakes. Abstract representations capture the ideational content of knowledge irrespective of the original input modality. Being language-independent, they are formalized in a propositional code specifying the meaning of assertions, thanks to a logical system called the *predicate calculus*; importantly, being *amodal* (i.e., not tied to any modality), they possess no isomorphic properties influencing performance (Anderson & Bower 1973; Pylyshyn 1973). In contrast, analog representations share with the reality they represent a

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first- or second-order isomorphism and are displayed on mental media preserving physical properties (e.g., spatial distances for visuo-spatial representations; Kosslyn et al. 1978). Because the processes acting on analog representations are sensitive to these properties, they can be traced in behavioral performance. Using criteria from seminal papers in cognitive (neuro)psychology, we highlight three important mistakes compromising CK&W's argumentation.

A first mistake consists in attributing the properties of the content of a representation (*representation of* [*object/concept X with properties P*]) to its format ([*representation of object/concept X*] *with properties P*; Pylyshyn 1978; 1981). Format and content being independent, content properties can be represented in modality-neutral and modality-specific formats (Caramazza et al. 1990). Stating that a numerical representation is abstract if behavioral effects depend only on magnitude is thus erroneous. Contrary to what CK&W write, McCloskey's semantic representation was not abstract because of its quantitative content, but because of its propositional format. Dehaene's magnitude representation on an analog medium provides the *a contrario* argument. Another common mistake concerns the inferences drawn from the (in)dependence between semantic representations and the various modalities/notations of access. Although abstract representations are amodal, a representation accessed through several modalities/notations is not necessarily abstract. Number semantics could be accessed from and give rise to similar effects in verbal, Arabic, or non-symbolic inputs while being non-abstract (e.g., Dehaene's analog representation). Conversely, modality/notation-specific effects do not necessarily sign non-abstract representations, because abstract representations could be accessed differently by modality-specific presemantic systems (Riddoch et al. 1988). By simply defining non-abstract representations as "sensitive to input modalities" (see sect. 2, para. 1), CK&W fail to provide a constraining framework. For example, finding that, after habituation, magnitude processing in one notation becomes more vulnerable to virtual lesions of the parietal cortex than in other notations, does not contradict the abstract view, as habituation could have modified the connectivity between notation-specific systems and abstract representations prior to the lesion. Trying to consider representations and processes separately constitutes CK&W's third mistake: Whatever their format, representations cannot be conceived as mental entities distinct from the processes acting upon them (Anderson 1976; Palmer 1978), and processes are totally determined by the format of the representations upon which they act (Shepard & Podgorny 1978). Therefore, any proposal of non-abstract representations must come along with a set of compatible processes clearly specified both at the functional and anatomical levels.

To properly assess the format of numerical representations, we make the following recommendations. First, a *data type* (a way of organizing information in memory; Simon 1978), and the primitive operations that can be performed on it, must be specified and supported by unambiguous behavioral effects. Rightward biases on the number line in neglect patients (Zorzi et al. 2002) is an instance of how intrinsic properties of representations may show through behavioral effects, but other frequently cited effects are not: The distance effect can be accounted by various types of representations (e.g., abstract semantic labels: Banks 1977; distributed representations: Verguts & Fias 2004), the congruity effect by a power-of-10-based propositional representation, and the SNARC effect by associations with abstract codes (Gevers et al. 2006c). Second, activations must be demonstrated in brain areas whose general cognitive role and pattern of activity are compatible with the assumed type of representation. For example, non-abstract representations tied to space predict numerical processes isomorphic to spatial orientation, with overlapping activations of number and space processing areas. Finally, a lesional approach must demonstrate that these areas are necessary to perform correctly the tasks relying on this representation. Indeed, non-abstract representations could simply be automatic by-products of mental activity and not its medium. CK&W's suggestion to rely on Stroop-like interference to infer the nature of numerical representations is thus irrelevant, because automaticity does not guarantee that the activated representation is functionally required.

The format of representations in memory is a major question in cognitive neurosciences. It was at the heart of the first architectures of numerical cognition, and CK&W should be commended for drawing our attention again to this critical but messy issue. Assessing the existence of abstract representations is a tricky if not impossible enterprise, because it boils down to demonstrating the absence of effects (e.g., of modality). Efforts should therefore rather be expended on testing possible candidates for non-abstract representations. However, although we believe that non-abstract numerical representations may have a true functional role, we think that the definitions and evidence provided by CK&W do not allow them to infer that numerical representations are non-abstract. We recommend using terms like "abstract/analog," "(a)modal," "supramodal," or "modality-(in)dependent," and so forth, with great care, because each of these conveys a specific meaning. Far from being a rhetorical question, this issue has strong theoretical and empirical implications. It is now time to overcome mistakes that hamper research on numerical representations and their relationship with the functioning of the human brain.

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Numerical representation, math skills, memory, and decision-making

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Abstract: The consideration of deliberate versus automatic processing of numeric representations is important to math education, memory for numbers, and decision-making. In this commentary, we address the possible roles for numeric representations in such higher-level cognitive processes. Current evidence is consistent with important roles for both automatic and deliberative processing of the representations.

The consideration of deliberate versus automatic processing of numeric representations is important to both math education and decision-making. Numeric information is ubiquitous in the decisions that we make, and thus numeric representation may play an important role. Basic number skills have only recently received attention in the decision literature. Numeracy, defined as the ability to process mathematical and probabilistic concepts, for example, has been shown to reduce susceptibility to framing effects and improve judgment accuracy (Peters et al. 2006). However, the effects of numeric representations in decisions have been largely ignored with two recent exceptions (Furlong & Opfer 2009; Peters et al. 2008). These lines of research raise important questions concerning relations between numeric representations, math skills, and the use of numeric information in decisions. This commentary adds to the Cohen Kadosh &

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Walsh (CK&W) viewpoint by addressing the possible roles of automatic and deliberate processing of numeric representations in higher-level cognitive processing.

Numeric representations and math skills. Peters et al. (2008) tested a large sample of healthy younger and older adults (mean age = 20 and 70 years, respectively) using a distance-effect reaction-time task with Arabic integers and dots ("Is the quantity shown bigger or smaller than 5?"), among other notations. In a reanalysis of the younger-adult data including only these two notations, the size of the distance effect varied by notation, with more precise representations (smaller distance effects) for Arabic integers than dots, supporting CK&W's point that numeric representations are not necessarily abstract. CK&W claim further support from findings that the distance effect with integers relates to math achievement, but the distance effect with dots does not. However, in the reanalysis of Peters et al.'s data, more precise numeric representations for both Arabic integers and dots were associated with higher numeracy scores. Halberda et al. (2008) demonstrated a similar positive relationship between 14-year-old children's performance on a task that used only numerosities (dots) and their math ability back to kindergarten.

The question remains whether this association is based on automatic or deliberate processing of the representations. An age comparison may be illuminating because of the shift that occurs in reliance on more deliberative to more automatic processes from younger to older adulthood across a variety of domains. If the relation between numeracy and numeric representations is based on more automatic processes, then this correlation should increase, as older adults tend to rely relatively more on automatic processes (see Peters et al. 2007 for a review); if it is based on more deliberative processes, one might expect a decreased correlation. In Peters et al.'s (2008) original data, the distance effect was less associated with numeracy for older than younger adults ($r = .06$, $p = .64$ and $r = .41$, $p < .001$, respectively). These data best support deliberate processes underlying numeracy's association with numeric representations. In addition, Castel (2007) found that older adults who were accountants and bookkeepers demonstrated memory ability remarkably similar to younger adults for arbitrary numbers, but not for arbitrary non-numeric information (where the usual age declines in memory were found). In another study, older adults were exceptionally good at remembering grocery-store prices, but not arbitrary prices (Castel 2005). Such data could support a more precise abstract representation for these individuals (who have more experience with numbers in general or grocery prices in particular) that is carried into later life. However, in combination with Peters et al.'s data, these findings are also consistent with motivated selectivity in deliberative processing (Hess 2000), with some numeric information (or all numbers for some individuals) being particularly important and valued.

Numeric representations and decision-making. In accord with CK&W's notion of a deliberate level of numeric representations, decision-makers are thought to use numeric information intentionally and deliberatively (e.g., stock-market indicators, mortgage rates, and grocery bills). Because human decision-making likely derives in part from the same mechanisms evolved by other animals in response to risky natural environments, intuitive representations of symbolic numbers should relate to how individuals respond to numeric information in decision-making. Peters et al. (2008) developed and tested hypotheses relating an individual-difference measure of the size of the distance effect to decision-making. They hypothesized that individuals with more precise representations would weight proportional differences between numeric attributes in choice more than individuals with less precise representations. In addition, a larger proportional difference should result in a bigger difference between individuals than a smaller proportional difference.

Results of two decision studies in Peters et al. (2008) supported these hypotheses. In the first study, individuals with more precise representations (compared to those with less precise representations) were more likely to choose larger prizes received later than smaller, immediate prizes, particularly with a larger proportional difference between the two monetary outcomes. In a second study, they were more likely to choose a normatively worse option that saved a greater proportion of lives at risk (but a smaller number of lives) compared to those with less precise representations. Importantly, these findings were more consistent with the abstract-representation view, because the results of both studies held after controlling for numeracy and various measures of intelligence associated with prefrontal activity. The precision of number representations appears to underlie: (a) perceived differences between numbers, (b) the extent to which proportional differences are weighed in decisions, and, ultimately, (c) the valuation of decision options. Human decision processes involving numbers important to health and financial matters may be rooted in elementary, biological processes shared with other species, and which depend on an automatic representation of numerical information across notations.

It is critical to better understand number representation in the context of how individuals use numbers. The CK&W article forces us to consider whether the role of these representations in higher-order cognitive processing emerges from a shared representation across notations resulting more from prefrontal activity or whether their role results from an abstract representation. The current results are most consistent with numeracy being related to the former shared representation and decision-making being associated with the latter automatic processing of the representations. Human decision-making, however, often involves prefrontal activity (Rangel et al. 2008), and further consideration of numeric representations being some combination of abstract and deliberate may converge with and ultimately explain some findings in the neuroanatomy of decision-making. It remains plausible that a shared deliberate representation (that is separate from what is associated with numeracy) could explain Peters et al.'s findings. A better understanding of the automatic versus deliberate nature of these representations' influences on decision-making will illuminate the important contribution of numeric representations on everyday decisions and should ultimately lead to improvements in decision aids.

What is an (abstract) neural representation of quantity?

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Abstract: We argue that Cohen Kadosh & Walsh's (CK&W's) definitions of neural coding and of abstract representations are overly shallow, influenced by classical cognitive psychology views of modularity and seriality of information processing, and incompatible with the current knowledge on principles of neural coding. As they stand, the proposed dichotomies are not very useful heuristic tools to guide our research towards a better understanding of the neural computations underlying the processing of numerical quantity in the parietal cortex.

According to Cohen Kadosh & Walsh (CK&W) a neural representation of quantity is abstract if "neuronal populations that code numerical quantity are insensitive to the form of input in which the numerical information was presented" (sect. 2, para. 1). This

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definition is extremely shallow; it does not state at what level the hypothesized neural code takes place; and it fails in taking into account that different attributes of stimuli may be coded by separate yet interconnected brain areas, by separate yet interconnected neuronal populations within the same brain area, or by exactly the same neuronal populations, yet with different tuning schemes (deCharms & Zador 2000). Indeed, in the specific case of the comparison between symbolic and non-symbolic numerical processing, we have proposed that our observation might be compatible with a common quantity code instantiated in the firing of a common set of parietal neurons with different tuning schemes for different input formats (finer tuning schemes for symbolic and broader tuning schemes for non-symbolic stimuli), as also predicted by a powerful computational model of number processing (Dehaene 2007; Piazza et al. 2007; Verguts & Fias 2004).

On CK&W's view, how should such quantity code be defined – as abstract or non-abstract? At what level(s) does abstractness need to be present for a given representation to be qualified as abstract? What if there are neural populations within parietal cortex that encode the quantity aspect of each notation separately, but that these populations are so deeply interconnected that the spread of the activation is automatic and the resulting larger scale population code appears as invariant to modality? In this case, the abstractness of the coding would almost literally be in the connections. Would this mean that the emerging population code is non-abstract? Despite the absolute centrality of these issues, this discussion is not even approached, and the existence of different possible levels of neural coding are not even considered. To us, this reflects an extremely naïve approach to a question (on what is a neural code) that is central and highly debated in the current neuroscientific literature. As a result, the dichotomy between abstractness versus non-abstractness seems like a very weak heuristic tool for our ability to answer the most meaningful issue, which is to unveil the computational principles underlying processing of numerical quantity in parietal cortex.

We also feel uncomfortable with the more general definition of neural representations in this target article. CK&W define their view of neural representations in extremely vague terms ("patterns of activation within the brain," sect. 2, para. 2), but in the rest of the article their operational definition of neural representations appears to be grounded on implicit views inspired by the classical cognitive psychology notion of module (Fodor 1983). Despite overtly criticizing the idea of neural module, CK&W actually embrace two important aspects of the classical definition of module: encapsulation (which here implies seriality of information processing), and domain selectivity.

The assumption of encapsulation and seriality is evident in CK&W's strict use of the additive factor method, for which the presence of statistical interactions between quantity-related effects and notation effects is taken as evidence in favor of notation-specific quantity representations. In light of our most recent knowledge of fine brain structure and function, encapsulation and seriality are extremely difficult to maintain. It is a known fact that different and also distant brain regions are massively bidirectionally interconnected and work in parallel (Felleman & Van Essen 1991). Not surprisingly, models that do take into account some degree of parallel processing show that interactions between factors can occur even if the factors affect completely separate processing stages (McClelland 1979; Rumelhart & McClelland 1986). This can happen, for example, if one factor affects one aspect of the information processing (say, the rate of evidence accumulation), and the other factor affects another aspect (say, the decision threshold). More refined data analysis taking into account precise response distributions and testing alternative (and more neurally plausible) models are therefore necessary before driving conclusions on the basis of scattered reports of (often weak) statistical interactions between factors.

Second, CK&W implicitly link abstractness to domain-selectivity. Thus, the fact that brain regions or individual neurons that are modulated by numerical quantity may also be modulated by other quantity- as well as non-quantity-related parameters, like physical length (Tudusciuc & Nieder 2007), color (Shuman & Kanwisher 2004), or motion direction (Nieder et al. 2006), is taken as undermining the possibility of an abstract representation of quantity. We disagree with this view.

In the first place, selectivity might be a property that arises at some level of neural coding that is not yet probed by most current methods of investigation (but see Tudusciuc & Nieder 2007). For example, in the case of numerical quantity, it is possible that numerical quantity-selective representations do exist, but emerge only as the averaged population activity of numerical quantity-*sensitive*, but not *selective* neurons. This would be the case, if, for example, some neurons respond both to number and length, others to both number and motion direction, and others to both length and motion direction (Nieder et al. 2006; Pinel et al. 2004; Shuman & Kanwisher 2004; Tudusciuc & Nieder 2007). Under this scenario, at the population level the codes for number, length, and motion direction would be distinct, but neither the single neuron spiking activity nor the functional magnetic resonance imaging (fMRI) signal averaging across all three populations would reveal such selectivity. In this respect, multi-unit recording allowing population coding properties to be more clearly unveiled, and multivoxel pattern analysis of the fMRI signal, capitalizing on very small variations in domain specialization across voxels, might reveal population codes which are indeed selective (Kamitani & Tong 2005; Tudusciuc & Nieder 2007). Alternatively, because of massive local connectivity, functional selectivity may only be revealed by taking into account long-range connections between distant brain regions. In either case, the issues of selectivity and of abstractness are two orthogonal ones. In conclusion, we think that reasoning in terms of ill-defined dichotomies (selectivity vs. non-selectivity, abstractness vs. non-abstractness) may induce unnecessary over-simplifications and is very unlikely to bring us towards a deeper understanding in this domain.

Abstract or not? Insights from priming

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Abstract: Cohen Kadosh & Walsh (CK&W) argue that numerical representation is primarily non-abstract. However, in their target article they failed to consider recent behavioral priming experiments. These priming experiments provide evidence for an abstract numerical representation under automatic conditions.

Recently, there has been a growing consensus favoring an *abstract* representation of numerical magnitude. According to Cohen Kadosh & Walsh (CK&W), this assumption might be premature, and they raise the alternative possibility that the default numerical representation is not abstract, but rather, dependent on notational input. CK&W argue that we will be more likely to observe evidence for a non-abstract representation under automatic processing conditions.

We applaud the idea of examining numerical representations under conditions of automatic processing, because then number processing is less affected by intentional strategies. However, based on research using the priming paradigm, the conclusion of CK&W is not supported. The priming paradigm is a very popular method to investigate underlying representations under

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highly automatic conditions. In a typical number priming paradigm, participants have to react on a target number that is preceded by a prime number while the numerical distance between both is systematically varied. Interestingly, when the numerical distance between prime and target is small (e.g., "1" preceded by "2"), the target is processed faster than when the prime-target distance is large (e.g., "1" preceded by "9") – that is, the priming distance effect. This effect was first shown by Den Heyer and Briant (1986) and later replicated under more automatic conditions using short stimulus onset asynchronies between prime and target and visual masking in order to eliminate strategic prime use (e.g., Reynvoet & Brysbaert 1999).

Certain priming studies manipulated the notation of prime and target: Prime and target were either presented in the same notation (e.g., prime "6" – target "7") or in different notations (e.g., prime "six" – target "7"). Originally, Koechlin et al. (1999) observed an interaction between notational change and distance priming: no distance priming effect was observed when prime and target were presented in different notations. This led to the proposal of notation dependent representations of quantity in line with the proposal of CK&W. However, the same group of researchers did observe cross-notation distance priming later on (Naccache & Dehaene 2001b), and they argued that the interaction effect obtained previously was a "spurious effect" and that "cross-notation priming is the norm rather than the exception" (Naccache & Dehaene 2001b, pp. 234–35). We ourselves (Reynvoet & Brysbaert 2004; Reynvoet et al. 2002) confirmed this observation of cross-notation priming in which magnitude processing was highly automatic (i.e., short stimulus-onset asynchronies between prime and target). Furthermore, we also extended this finding by showing cross-notation priming under conditions in which the target had to be named, which implies that the numerical magnitude was completely irrelevant for the task. In addition, we also demonstrated cross-notation priming under conditions in which the formation of intentional links between different notation-dependent representations is discouraged. In a first study, the targets were always presented in the same notation, while the preceding primes, invisible to the subjects, were presented in different notations. Still, a distance priming effect was observed when notation changed (Van Opstal et al. 2005a). In a second study, investigating the lexico-semantic system of trilingual speakers, we found distance priming when masked English number word primes (e.g., "three") were presented before a to-be-named Dutch (e.g., "twee") or French (e.g., "deux") number word target (Duyck et al. 2008). This cross-notation and cross-language priming provide convincing evidence for an abstract numerical representation under automatic conditions.

If behavioral priming supports the idea of an abstract numerical representation, how can we account for the interactions between number notations and magnitude-related effects observed using other paradigms reviewed by CK&W? It should be noted that many of the observed interactions are due to the (near) absence of the magnitude-related effects in particular conditions (e.g., Dehaene & Akhavein 1995; Fias 2001; Hung et al. 2008; Ito & Hatta 2004). These null results may be caused, for example, by differences in the strength of the associations between an input notation and the corresponding magnitude and/or spatial representations (see also Brysbaert 2005). Because of these notation-dependent associations, it could be that a magnitude-related effect is not observed for a particular notation, which results in an interaction when combined with other notations in an omnibus analysis. We believe that a better way to address the issue of notation-dependent representations is to look for positive results, and that is exactly what we did in our cross-notational priming experiments, where we found evidence for cross-notation priming in many experiments, even under highly automatic conditions.

In sum, much of the evidence in favor of a notation-dependent magnitude representation is based on a null effect in a particular condition. We reviewed a series of experiments using cross-notational priming that were based on the presence of an effect, that is, cross-notational distance priming. These results are in favor of an abstract magnitude representation and should be dealt with in any theory on numerical processing.

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Symbolic, numeric, and magnitude representations in the parietal cortex

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Abstract: We concur with Cohen Kadosh & Walsh (CK&W) that representation of numbers in the parietal cortex is format dependent. In addition, we suggest that all formats do not automatically, and equally, access analog magnitude representation in the intraparietal sulcus (IPS). Understanding how development, learning, and context lead to differential access of analog magnitude representation is a key question for future research.

We agree with Cohen Kadosh & Walsh's (CK&W's) central contention that representation of number in the parietal lobes is format dependent. The authors should be commended for presenting the clearest discussion yet of this topic, and for revisiting and reinterpreting findings from older studies. It is indeed surprising how many investigators have abandoned their own results only to reiterate staid theories. In this context, one is reminded of Ioannidis (2005): "[F]or many current scientific fields, claimed research findings may often be simply accurate measures of the prevailing bias" (p. 0696). By explicitly pointing out research biases extant in the literature, CK&W present the field with an opportunity to consider new interpretations and formulate more targeted research questions.

CK&W frame their review in terms of *abstract* number representations in the parietal cortex, as is the norm in the field. However, a more appropriate question is: How do various symbolic systems exploit magnitude-processing capacities of the intraparietal sulcus (IPS) and under what conditions? CK&W do not address exactly why, or how, numerical formats differ in the degree to which they evoke effects consistent with an analog magnitude representation. By focusing on the absence of transfer of magnitude information across formats, the authors appear to have overlooked more fundamental differences between formats that have roots in experience and development. Given that numerical symbols are cultural artifacts that are learned over time, we believe that not all formats will necessarily access analog-magnitude representations equally, and, in general, the degree to which a format has access to this representation depends on past exposure and current task context.

The findings reported by Cohen Kadosh et al. (2007b) in a two-trial adaptation paradigm are consistent with our view. This study found that presenting the same digit twice produced less activity in the right IPS compared to sequential presentation of two different digits. When the two numbers were presented in different formats (digit and number word), there were no differences

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in activity for same or different quantities, consistent with a format-dependent view. However, there was also no difference between same and different quantities when both numbers were presented as number words. This result is inconsistent with the view that number words are automatically represented as magnitudes in the IPS, a central assumption of both the abstract and non-abstract views.

One intriguing result from Cohen Kadosh and colleagues' (2007b) study is that although number words did not show numerosity-related adaptation, they did produce robust activity in the IPS, comparable to the level observed for digits. This suggests that the IPS can encode number words in a non-magnitude-dependent manner. Strong evidence for notation-dependent activity in the IPS also comes from neurophysiological studies: Diester and Nieder (2007) found that monkeys who had learned to pair digits with dots activated distinct neuronal populations for each format. However, some of the digit-selective neurons did not demonstrate graded tuning curves; instead they fired only for a specific digit (Diester, personal communication). These non-magnitude representations are potential precursors to the development of automatic analog magnitude representations. Consistent with this proposal were results from a training study by Lyons and Ansari (2009) in which participants learned a pairing of arbitrary symbols with approximate magnitudes. Although the IPS was active both early and late in training, and distance effects grew more pronounced with experience, only late in training did activity in the IPS correlate with individual differences in the size of the distance effect.

Our view is also consistent with existing behavioral data, including those cited by CK&W. For example, among Japanese participants, digits and Kanji numbers, but not Kana scripts, showed interference from numerical magnitude on a font size discrimination task (Ito & Hatta 2004). Like number words, Kana scripts may not evoke an automatic analog magnitude representation. This is possibly because Kanji numbers elicit magnitude representations in their visual form more so than Kana scripts (Kanji number symbols begin with one, two, and three (horizontal) lines and have closer ideographic connection to numerosities than do Kana script). In this case, differential degrees of magnitude representation could be due to limited experience with Kana scripts in the context of number processing. Context can influence magnitude representations, even within formats. For example, adults in the Mundurucu tribe produce behavior consistent with a compressed analog magnitude (i.e., logarithmic) for dot displays. Within verbal number words, Mundurucu words evoked logarithmic representations, whereas Portuguese words evoked linear representations (Dehaene et al. 2008). Grade-school-aged children have both linear and logarithmic representations on the same stimuli depending on whether they were in a 0–100 range or a 0–1000 range (Siegler & Opfer 2003). How these behaviors are represented in the brain is currently unknown, but we suggest that this involves more than the IPS – they are likely to depend on the context-dependent interaction of the IPS with the ventral visual stream and the prefrontal cortex (Wu et al. in press).

How can we disambiguate the view that different neuronal populations encode different formats with the same magnitude-based organization, from the idea that different populations have dissimilar analog-magnitude representations that are context- and experience-dependent? Longitudinal developmental research and learning paradigms, such as Lyons and Ansari (2009), could go a long way towards clarifying such questions. CK&W note that null effects have been over-interpreted as evidence of notation dependence – many studies may, in fact, have been grossly underpowered to detect notation-specific effects. Increasing sample sizes, particularly in imaging studies, would be a simple way to increase detection and improve interpretability and generalizability of research findings. Finally, feature selection and classification algorithms, which search for consistent patterns of activation between conditions, could potentially uncover differences between formats that would not be manifest in differences in overall levels of activation (Ryali & Menon 2009).

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Abstract representations of number: What interactions with number form do not prove and priming effects do

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Abstract: We challenge the arguments of Cohen Kadosh & Walsh (CK&W) on two grounds. First, interactions between number form (e.g., notation, format, modality) and an experimental factor do not show that the notations/formats/modalities are processed separately. Second, we discuss evidence that numbers are coded abstractly, also when not required by task demands and processed unintentionally, thus challenging the authors' dual-code account

A crucial part of Cohen Kadosh & Walsh's (CK&W) argument against abstract representations concerns the fact that different effects (e.g., distance, SNARC, compatibility effects) are often not quantitatively the same for different number forms like notation (e.g., Arabic vs. verbal), format (e.g., symbolic vs. non-symbolic), and modality (e.g., visual vs. auditory modality). For concreteness, we will here focus on the distance effect. The authors note that distance between two numbers in a comparison task interacts with notation: Cohen Kadosh (2008a), for example, reports that the distance effect is larger for numbers in Arabic notation than in verbal notation (notation–distance interaction). However, the fact that a common abstract coding system is accessed by different notations does not mean that the representation of these notations should be exactly equal. In a neural system, obtaining exactly the same representations for different notations would be possible only if the input pathways to the common coding system for the different notations are exactly the same, which is clearly impossible. If there is a common coding system, but some divergence between the input pathways to it, the activation pattern on the common system will be (at least slightly) different for different notations, and any effects downstream from the common representation will be influenced.

This also holds when number formats are different, in particular when comparing symbolic (Arabic, verbal) with non-symbolic (collections of objects) number formats. Computational modeling has suggested that there is a common abstract coding system for symbolic and non-symbolic formats (Dehaene & Changeux 1993; Verguts & Fias 2004), but that the input pathways for the two formats are different, with one format (non-symbolic number) being much more noisy and passing via an extra representational processing stage (Santens et al., in press). Because of this extra stage, there can again be different behavioral signatures for the two formats (e.g., format–distance interaction; Roggeman et al. 2007), even when they eventually converge on a common coding system. Finally, given that different modalities are processed by different sensory input systems, a similar argument holds for modality–distance interactions.

Having argued that the evidence against an abstract coding system of number is not convincing, we now turn to some positive evidence in favor of such a system. CK&W argue that it may exist, but only in limited circumstances, in particular when participants

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are required as part of the task demands to treat different number notations (or formats, or modalities) as similar, or when they (for whatever reason) intentionally choose to treat different notations as similar. To evaluate this claim, we look at number priming studies in which (1) prime and target numbers are presented in different notations (so numbers in the prime notation are not included in the task demands); and (2) it is explicitly demonstrated that primes are not consciously processed (so it is excluded that participants would intentionally create a cross-notation number system). In such studies, we can then check whether there is a cross-notation prime-target distance effect, which is commonly regarded as evidence for access of prime and target to a common semantic coding system (e.g., Reynvoet et al. 2002). At least two studies fulfill both criteria. Both studies used a number comparison task with a fixed standard for comparison. Reynvoet and Ratinckx (2004) used Arabic and verbal primes, but Arabic target numbers only, so verbal numbers were not included in the task demands. In their Experiment 2b, primes were shown to be not consciously perceived, so participants could not have intentionally included verbal numbers in their number set. When prime and target were both presented in the left hemifield (right hemisphere), there was no cross-notation priming effect; however, the effect was present in the right hemifield (left hemisphere). Hence, at least in the left hemisphere, there seems to be a common coding system, even when it is not required by task demands and outside participants' intentions. Second, in the study of Van Opstal et al. (2005a), primes were presented in both notations (verbal and Arabic), and targets were presented in one notation only (either verbal or Arabic, varied across participants), so participants were again performing the comparison task on one notation only. Primes were demonstrated to be unconscious, so they were also aware of one notation only. A prime-target distance effect was present in this case (reported in Van Opstal et al. 2005b). Further detailed analysis of this effect showed a significant cross-notation prime-target distance effect when primes were Arabic and targets were verbal ($F(1, 21) = 8.59$, $p < .01$). The prime-target distance effect was not significant when primes were verbal and targets were Arabic ($F(1, 21) = 1.64$, $p = .21$), perhaps because verbal stimuli less easily survive visual masking (cf. Reynvoet & Ratinckx 2004). Whatever the reason, these priming studies demonstrate cross-notational, semantic priming even under circumstances in which participants do not consciously perceive the prime notation during the whole experiment.

To sum up, interactions of an experimental factor like distance with notation, format, and modality are not informative with respect to the existence of an abstract coding system; cross-notation priming effects are, and they demonstrate that such a system exists.

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Beyond format-specificity: Is analogue magnitude really the core abstract feature of the cultural number representation?

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Abstract: The issue of abstractness raises two distinct questions. First, is there a format-independent magnitude representation? Second, does analogue magnitude really play a crucial role in the development of human mathematics? We suggest that neither developmental nor cultural studies support this notion. The field needs to redefine the properties of the core number representation as used in human arithmetic.

Can magnitude really be considered the core abstract defining feature of numbers as cultural products? We argue here that developmental and other evidence is against this notion. We agree with Cohen-Kadosh & Walsh (CK&W) that numerical representation is primarily not format-independent. However, we propose that a clear distinction must be made between an evolutionarily grounded sense of approximate magnitude (Dehaene 1997) and a different, culturally acquired, abstract number concept. We propose that what the field requires are criteria to define the abstractness of the number representations as used by humans in mathematics.

In support of CK&W, data of our own suggest that numerical coding is dependent on surface format. Szűcs and Csépe (2004) presented two numbers (N1 and N2) using consecutive visual presentation. Participants were asked to add the numbers and to decide whether or not the proposed sum was correct. N1 could be presented as an Arabic digit or as a visual word, or acoustically as a heard number word. N2 was always an Arabic digit. The modality of N1 had a systematic effect on the amplitude of event-related brain potentials measured at N2. These data suggest that N1 was not translated into a common abstract number representation. Rather, N1 was retrieved from modality-specific stores when needed. Alternatively, both abstract and modality-specific stores may be involved in coding numbers.

Similarly, the functional magnetic resonance imaging (fMRI) evidence to date does not necessarily provide clear evidence for a core common magnitude representation. Current imaging studies may map the comparison process rather than overlapping representations. For example, the most frequently used marker of the putative magnitude representation is the numerical distance effect. Phenomenologically similar distance effects with various stimulus materials do not in themselves imply a single underlying neural representation. Specifically, Pinel et al. (2004) have shown that comparing numbers and physical size results in overlapping distance effects in terms of brain activity. Hence, they assume a shared representation for numerical and physical magnitude. But it may be the *processes* operating on these representations that overlap in terms of brain activity. Number magnitude and physical size may be represented in non-overlapping brain areas, with overlapping brain areas involved in the *process* of size comparison rather than the representation of abstract magnitude. Indeed, fMRI distance effects are rarely constrained to the intraparietal sulcus (Szűcs et al. 2007). Hence, a single abstract representation is difficult to define in terms of a simple anatomical hypothesis.

As CK&W note, neural adaptation studies do not provide unambiguous evidence either. Neural adaptation studies supporting an abstract magnitude representation are based on repetition priming and do not require participants to carry out comparisons. This research design excludes confounds related to comparative activity. However, a problem inherent to adaptation paradigms still remains. As Naccache and Dehaene (2001a, p. 967) state, this is a "general problem of potential strategical or attentional changes elicited by the awareness of repetition." Hence, "ideally experimental designs based on the priming method should prevent subjects from becoming aware of the presence of repeated versus non-repeated trials" (p. 967). In other words, in number adaptation paradigms participants may direct attention to the numerical dimension, even if they are instructed not to. Hence, adaptation results will be confounded by simple change detection effects. Such confounds are especially likely when participants are instructed explicitly to

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"pay attention to the quantity conveyed by the stimuli" (Piazza et al. 2007, p. 303) or when symbolic numbers are used (Cohen Kadosh et al. 2007b). A published exception is the study of Naccache and Dehaene (2001a), which used symbolic stimuli and combined the adaptation paradigm with masked priming, so that participants were not aware of any stimulus repetitions. However, this result to date remains unreplicated.

Developmentally, it is important to ask whether a sense of magnitude is actually important in order to carry out successful arithmetic. So far, developmental studies have demonstrated that magnitude comparison performance does not correlate with early arithmetic skills beyond 3–4 years of age (Brannon & Van de Walle 2001; Mix 1999; Mix et al. 1996; Rousselle et al. 2004). This raises the possibility that magnitude discrimination skills do not play a crucial role in the development of the cultural number concept.

For example, Halberda et al. (2008, p. 666) claimed that magnitude comparison skill in ninth grade "retrospectively predicted" symbolic maths performance. Hence, they concluded that the magnitude representation "may have a causal role in determining individual maths achievement." However, this inference is problematic, as magnitude comparison was measured at age 14, whereas arithmetic performance was measured between ages 5 and 11. Hence, it is equally possible that better mathematics skills caused better magnitude performance. This conclusion is actually supported by the data from Amazonian Indians. These data showed that Indians have marginally worse magnitude discrimination skills than adults educated in Europe (Pica et al. 2004). It seems unlikely that Amazonian Indians are worse in symbolic maths than Europeans because their number sense is genetically limited. A more plausible explanation would be that Europeans' number discrimination skills are better because they are educated. In fact, if we assumed that there was no difference between Indians and Europeans (given that the difference was marginal), the conclusion would again be that number discrimination skills have no relationship to mathematical skills (as the latter would be expected to be better in educated Europeans).

Therefore, both methodological and theoretical problems surround the notion of an abstract number representation. Furthermore, a distinction may be needed between an evolutionarily grounded approximate sense of magnitude (Dehaene 1997), whether abstract or not, and a distinct, culturally acquired abstract number concept. CK&W cite Barsalou (2003), "abstraction is simply a skill that supports goal achievement in particular situations" (p. 1184). Given that the goal of mathematics education is to teach children an abstract number concept, the real question would seem to be whether this putative abstract core number representation bears any relation at all to the analogue magnitude representation.

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In search of non-abstract representation of numbers: Maybe on the right track, but still not there

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Abstract: We agree that the default numerical representation is best accessed by probing automatic processing. The locus of this representation is apparently at the horizontal intraparietal sulcus (HIPS), the convergence zone of magnitude information. The parietal lobes are the right place to look for non-abstract representation of magnitude, yet the proof for that is still to be found.

Cohen Kadosh & Walsh (CK&W) focus on the mental representation of numbers. They do not state it explicitly, but it is clear from their argument that they are interested in the default internal representation of an external stimulus that corresponds to a specific magnitude. It should be distinguished from "working representations" generated to perform specific tasks. This default representation symbolizes magnitude as stored in semantic memory and is sometimes described in terms of the "mental number line" (e.g., Restle 1970). The authors suggest that the locus of this representation is in the parietal lobes and propose that it is best probed by automatic processing of numerical information. The authors review the existing data and conclude that it does not allow a conclusion in favor of an abstract representation of numerical information. As an alternative, they propose that numerical processing starts with non-abstract representation (coded by different neuronal populations for different categories/modalities of inputs) in the parietal lobes, which is automatic in the sense of not being affected by task requirements. Abstract representations may emerge later in the prefrontal cortex (PFC) as a result of the task requirements.

Whatever the representation of numerical information in the brain is, it codes the relevant features of the mental number line, such as the increased discriminability between magnitudes farther away from each other, known as the distance effect, and, for a given intra-pair distance, better discrimination for pairs of small numbers, known as the size effect (e.g., Moyer & Landauer 1967). The size congruity effect (SiCE) is frequently used as a marker of automatic processing of numerical information (e.g., Tzelgov & Ganor-Stern 2005). It refers to shorter latencies of physical size decisions when the presented physically larger number is also numerically larger (congruent condition, e.g., 5 3) than when it is numerically smaller (incongruent condition, e.g., 3 5). The SiCE increases with the intra-pair numerical distance (e.g., Tzelgov et al. 2000), and is larger for numerically smaller pairs (Cohen Kadosh et al. 2008g, but see Van Opstal et al. 2008; Verguts & Van Opstal 2008; Verguts et al. 2005). Thus, conceiving magnitudes means activating the mental number line and mapping the specific magnitudes on it.

We do not believe that representation of magnitudes in general, and numbers in particular, can be reduced to the neural activation of specific populations of neurons. Another definition of the representation of magnitudes would be in terms of the relevant neural circuit activated when information in a given domain (e.g., numerical) is processed. Dehaene et al. (2003) pointed out that the horizontal intraparietal sulcus (HIPS) is activated by numbers independently of their notation, and proposed it as the neuronal locus of the mental number line. Thus, while specific populations of neurons are the locus of activation of feature detectors for different kinds of stimuli corresponding to magnitudes, it seems to us that the HIPS is a possible candidate for the convergence zone (Damasio 1989) for magnitude information. It follows that even if different populations of neurons fire for different kinds of inputs, magnitude is represented once the HIPS is activated. In this sense, the network resulting from the convergence of the stimulus-specific neuron populations, corresponding to various kinds of quantities and numbers in various notations, whose activation converge in the HIPS, generates what Barsalou (1999; 2005) calls a simulator. It simulates the "mental number line," and while it may be based on perceptual symbols (Barsalou 1999), it summarizes the magnitudes specifically coded by the various populations of neurons. In this sense, while the automatically probed numerical representations may be non-abstract in the sense of being based on the firing of different population of neurons, they are

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"abstract" in the sense of summarizing the different inputs by the HIPS. Although, according to CK&W, the existing data do not allow for a clear conclusion in favor of an abstract representation, they do not support the opposite conclusion, either.

Only numbers that are stored in memory as part of the mental number line can be automatically activated, that is, retrieved from memory without intentional effort (Logan 1988; Perruchet & Vinter 2002). According to findings from our lab, the set of numbers included on the mental number line is quite limited. It seems that the mental number line represents only single-digit positive integers, that is, it does not include two-digit numbers (Ganor-Stern et al. 2007), negative numbers (Tzelgov et al. 2009), or fractions (Kallai & Tzelgov, in press). Thus, the single-digit positive integers may be considered as the "primitives" of numerical cognition, and are automatically accessed (or "retrieved from memory").

The representations of numbers that are not part of the mental number line are generated on-line, when needed, by intentional operations. They are generated as part of "working representations," as a result of intentionally applying task-relevant operations on the "primitives" included on the mental number line. The prefrontal cortex is apparently active in this process, as it is in additional operations that involve numbers, such as arithmetic (Ansari 2008). Therefore, neural activity in the prefrontal cortex reflects the working representations heavily loaded by the task requirements. Thus, while we agree with CK&W that probing automatic processing should provide the answer to the question of whether the representation of numerical information is abstract, we emphasize that this should be done by analyzing the numbers that are members of the mental number line. The data that one can accumulate according to these criteria, at this point are not strong enough for the rejection of a hypothesis of abstract representation of numerical information.

Numerical representations: Abstract or supramodal? Some may be spatial

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Abstract: The target article undermines the existence of a shared unitary numerical format, illustrating a variety of representations. The "abstract"/"not-abstract" dichotomy does not capture their specific features. These representations are "supramodal" with respect to the sensory modality of the stimulus, and independent of its specific notation, with a main role of spatial codes, both related and unrelated to the mental number line.

In their article Cohen Kadosh & Walsh (CK&W) review an extensive psychological and cognitive neuroscience literature, with the aim of showing that, contrary to the dominant view put forward by McCloskey (1992) and Dehaene et al. (1998a), numeric representations are primarily not abstract. The process of abstraction of numbers has a long story (Schmandt-Besserat 1999), starting circa 8000 B.C. from a one-to-one correspondence between three-dimensional tokens (e.g., an ovoid) and units (e.g., a jar of oil), and finally developing, through successive stages, into the current "abstract" numerical representation, which is discussed by CK&W. What CK&W mean by "abstract" is that the relevant representation conveys information only related to the size of the numbers involved, independent of the particular number notation (symbolic: number words or Arabic digits; non-symbolic: e.g., dot patterns), and of the sensory modality of presentation of the stimuli (auditory, visual, somatosensory) (Libertus et al. 2007). Over and above its semantic nature, the specific format of such an "abstract" numerical representation has been regarded as primarily propositional by McCloskey (1992), while Dehaene et al. (1998a) have emphasized its spatial characteristics.

CK&W's review, more than focusing on what is promised by their title ("Numerical Representation: Abstract or not Abstract?"), presents evidence drawn from a variety of experimental paradigms to the effect that, under specific experimental conditions and task requirements, different numerical representations may be generated. The conclusion here is that "multiple" representations versus a "single" or "shared" numerical representation exist in the brain. More specifically, CK&W suggest that a shared numerical representation does not exist as default, but may result by connecting on-line multiple representations only when intentional processing of numbers occurs. This shared versus multiple numerical representation distinction, however, speaks little as to the abstract/non-abstract dichotomy, unless the relevant representational formats are specified. In particular, as CK&W note, it is generally assumed that the occurrence of a behavioral effect, as for example the SNARC effect, across different notations (Nuerk et al. 2005), speaks in favor of a unique numerical "abstract" representation. The fact that the SNARC effect is independent of notation or modality may well suggest that it comes from the activation of a unique "supramodal" representation – but this says little about its abstractness.

For example, in the experiments by Bächtold et al. (1998), the observation that the SNARC effect is preserved when numbers are conceived as distances on a "ruler," but reversed when they are conceived as hours on a "clock-face," suggests the existence of distinct numerical representations. These results indicate that the involved representation is primarily "spatial," rather than "abstract," as shown by the observation of a SNARC ("ruler" condition), and of a reversed-SNARC ("clock-face" condition) effect, as well as flexible enough to be modulated by the experimental instructions (i.e., ruler, mental number line-related, vs. clock-face). Accordingly, Bächtold et al. (1998) discuss their results in terms of spatial stimulus-response factors, which may be conceived as analogical processes, rather than with reference to "abstract" versus "non-abstract" codes.

Other studies suggest the existence of "supramodal," "non-abstract" numeric representations, independent of the mental number line, and affecting spatial processes. De Hevia et al. (2006), using a manual line bisection paradigm, found that neurologically unimpaired participants displace the subjective midpoint of lines and of unfilled spaces, flanked by two different Arabic numbers (e.g., 2–9, 9—2) towards the larger digit, independent of its left-sided or right-sided position. This effect is not modulated by numerical distance, making unlikely an interpretation in terms of mapping onto a mental number line. These findings may be accounted for by the hypothesis of a "cognitive illusion," largely independent of the allocation of attentional resources, whereby visually presented larger digits are associated with an expansion of the closer portion of space, be it a segment or an empty space. This "position of the larger number" effect reflects the processing of relative numerical magnitude, since the bisection of horizontal strings composed by larger or smaller digits (i.e., absolute numerical magnitude) does not modulate bisection according to a mental number line effect, namely, with leftward/rightward errors associated with smaller/larger numbers, as found by Fischer (2001). In a later study, de Hevia et al. (2008) extended these findings that larger numbers are associated with an expansion of spatial extent, using a task whereby participants were required to reproduce

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the perceived length of an empty space, delimited by pairs of smaller/larger digits. De Hevia and Spelke (2009) have recently replicated and extended these findings, using not only pairs of visual digits flanking a line, but also non-symbolic visual displays, for example, with nine smaller circles denoting a larger numerical magnitude, and two larger circles a smaller magnitude. With non-symbolic displays, adult participants, young school (7-years-old), and preschool (5-years-old) children show a line bisection bias towards the larger numerical magnitude. With symbolic cues (digits), the deviation towards the side of the larger digit is present in adult participants, but not in 7-year-old children. Taken together, these findings suggest the existence of a "supramodal" (i.e., independent of the particular format of the stimulus) representation of numerical magnitude – unrelated to the mental number line – which modulates spatial representations. With reference to the operational definition adopted by CK&W, this representation is "abstract," being accessed by different notations. We would however qualify this representation – present as early as in 5-year-old children – as "supramodal" or, more precisely, "notation-independent," and closely related to, or possibly overlapping with, spatial representations.

In conclusion, CK&W's review is definitely successful in showing that multiple numerical representations exist. The empirical data we have briefly reviewed here, however, indicate that the "abstract"/"not-abstract" dichotomy is too general to capture the variety of possible supramodal numerical representations, to which spatial codes provide a main format.

Do infants count like scientists?

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Abstract: We discuss methodological problems and present our own empirical data on calculation tasks in toddlers. We propose to develop enriching theoretical models concerning quantity representations, based on empirical findings from developmental psychology. A revitalization of the debate is worthy, because it is reminiscent of the philosophical dispute on universal entities in scholasticism and Plato's theory of ideal numbers.

Cohen Kadosh & Walsh (CK&W) brilliantly discuss methodological and theoretical limitations of neurophysiological evidence supporting the claim that numerical representation is abstract. However, this reasoning can also be applied to their own arguments:

1. Finding no difference in BOLD signal intensity in functional magnetic resonance imaging (fMRI) studies between different modalities ("null result") may be due to a lack of statistical power. However, even by increasing the statistical power (i.e., increasing the number of subjects, or the intensity of the paradigm, respectively), thus potentially resulting in a significant difference in BOLD signal between different forms of input, would not necessarily imply a relevant notation-dependent cortical output (Logothetis 2008).

2. Single-cell neurophysiology does not solve the problem of reduced spatial resolution of fMRI experiments, because only a small portion of neurons in a specific brain region can be explored using this technique.

3. Although single-cell physiology is used in clinical settings (e.g., Engel et al. 2005), single-cell *experiments* are not yet applicable to *humans*. Thus, this method cannot yield direct evidence of a non-abstract numerical representation in the *human* brain.

4. The fact that CK&W address single neurons as abstract or non-abstract neurons is questionable. First, any understanding of abstract representations as neuronal populations that are insensitive to the form of input does not imply the existence of *abstract* neurons. Second, how do the authors classify a mental representation localized in a specific brain region, including abstract and non-abstract neurons that are highly co-located?

Despite these methodological concerns, we share the authors' doubts that an abstract number representation exists in the human brain. According to recent developmental approaches, preverbal infants, as well as monkeys, have two different systems for representing quantitative information: one system for small numbers of objects that can be tracked over space and time, and one system that represents large, approximate numerosities (Spelke 2000). Both systems are independent of verbal information processing and apply to different sensory modalities, stimuli, and task contexts. In that sense, one could say that they are abstract. But this is not the type of abstract representation that CK&W talk about. The authors focus on an adult number concept.

In order to communicate about number representations in an adult-like way, young children must learn to (a) abstract the general meaning of number words as representations for quantities, (b) say number words in the correct sequence, (c) identify number symbols, and (d) associate words as well as digits with exact quantities. To form some sense of a number scale, they also need experience in bringing exact quantities in a linear order. Children who have already acquired basic counting skills cannot yet solve mathematical equations, but are able to solve the same problems using less abstract representational formats. This can be illustrated by data from our own laboratory (Pauen, in preparation).

A study with 138 4–5-year-olds tested performance on simple addition problems involving small numbers ($x < 10$). Four different task formats were presented: (1) Real objects: Children were shown two groups of objects and were asked, "How many marbles are there together?" (2) Object words: No object was presented, but children were asked the same kind of question as before, combining object and number words, for example, "How many are one banana and five bananas together?" (3) Number words only: For example, "How many are three and three together?" As revealed by our Figure 1, performance systematically varied with task format. Performance was highest when real objects were presented, lower for questions combining object and number words, and very low when only number words were involved.

These findings illustrate that number operations strongly depend upon how numerosities are presented at preschool age. With the beginning of elementary school training, task format gradually loses importance and children learn to flexibly shift from one format to another.

Based on developmental research, one can conclude that there is no such thing as an innate abstract representation for exact numbers in terms of their representation format (words, digits, quantities). The cognitive subsystems involved in processing different types of numerical information seem to be distinct at the beginning. They become gradually associated as a result of repeated exposure to simultaneous presentation of different representation formats (e.g., number words combined with specific object quantities and/or digits).

In summary, we argue that two distinct innate systems representing small numbers of objects and large quantities may exist, and that they are not tied to any verbal or visual symbols of numbers (Spelke 2000). Hence, they are abstract in a different sense than that defined by CK&W. A more elaborate representation of exact numbers evolves by forming associations between exact quantities and symbolic systems identifying digits and numbers during preschool years.

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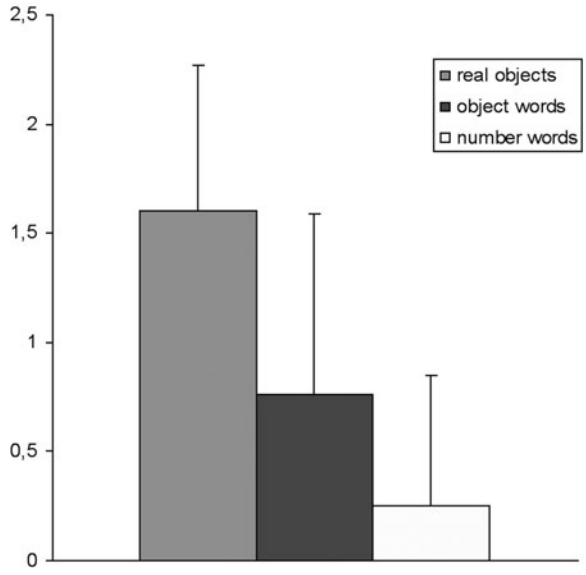


Figure 1 (Wiefel et al.). Mean number of correct answers for two simple addition problems presented in three different task formats (real objects, object words, number words).

Based on this conclusion, we think that the work of CK&W could be extended by taking into account a developmental (ontogenetic) perspective. Could it be useful to combine the authors' theoretical approach with the knowledge about the emergence of representation in infancy? This might mean that a representation of quantities is more basic than a representation of exact numbers. Fonagy and Target (2003) claim that we need "something more" than knowledge about cognitive-behavioral pathways for understanding representations/mentalization in general. This could be a key to understanding why neuroimaging alone does not reveal how numbers/quantities are represented in the human mind. May the results from paradigms of preferential looking in the newborn and early infancy period (infants love "A" *more* than "B"; e.g., Meltzoff 1990) represent the pre-existence of abstract quantities? Could this be reminiscent of the philosophical dispute on universal entities in scholasticism ("*universalia sunt ante res*")? This question is associated with Plato's theory on the existence of *ideal numbers*. The Renaissance of this in Neo-Platonism contributes to the current scientific debate. It could be enriched by further trans-disciplinary research between neuroscientists, developmental psychologists, clinical practitioners, and philosophers.

Authors' Response

Non-abstract numerical representations in the IPS: Further support, challenges, and clarifications

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Abstract: The commentators have raised many pertinent points that allow us to refine and clarify our view. We classify our response comments into seven sections: automaticity; developmental and educational questions; priming; multiple representations or multiple access(?); terminology; methodological advances; and simulated cognition and numerical cognition. We conclude that the default numerical representations are not abstract.

So, do we represent numbers non-abstractly? We appreciate the tone and the quality of the commentaries on our target article in general. The commentators provided us with a mixed view: Only 7 commentators defend the abstract view, 11 commentators are agnostic and their arguments tend toward the non-abstract representations or abstract representation, and 10 commentators support the idea that numerical representations are non-abstract. Clearly, our view has facilitated an important debate. In this response, we integrate the different positions, explain why some of the arguments against the non-abstract view are invalid (mainly based on clarifications of arguments that we provided in the target article), and conclude that the default representations of numbers are non-abstract.

R1. Automaticity

Algom raised important concerns, and contentious topics. Before dealing with his main points, we would like to point out several places in his commentary where our perspective was extended to places that we did not state in our article. It might be that we were not clear enough on these topics in our article, and for some of the readers these misinterpretations might be minor, but we would like to state them for the sake of theoretical clarity. We neither said nor believe that numerical magnitude is processed automatically whenever a numeral is presented for view. This is a very strong definition of automaticity, and Algom and others have shown that such a definition of automaticity does not hold. We also did not state that Stroop-like tasks are the best behavioural tasks to reveal the effect of notation on numerical magnitude. We do believe that there are some advantages for using this paradigm (and also some disadvantages).

Cohen and **Algom** describe findings by Cohen (2009), in which the physical shape, rather than the numerical magnitude, was processed. There is no reason to be surprised by this result. If the physical shape is more salient than the numerical magnitude, it will mask the effects of the numerical magnitude. We expect that the reverse will be obtained if the numerical magnitude is made more salient using the same paradigm.

The other point that **Algom** mentioned is one raised some years ago, researched extensively, and we believe, refuted. Algom states that,

> virtually all studies that demonstrated the effect (of task-irrelevant numerical magnitude on judgments of physical size [i.e., size congruity effect]) used a design that favored the numerical over the physical dimension in the first place. Thus, more values of number than values of physical size were typically presented (indeed, most studies used merely two values for size: large, small) [termed variability]. Moreover, the numerals were easier to discriminate from one another than their physical sizes [termed discriminability]. (Our explanations added to Algom's in square brackets.)

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These are potential problems that Algom has raised previously (Algom et al. 1996; Pansky & Algom 1999; 2002), and that were ignored by some researchers, including us (Cohen Kadosh et al. 2007d; Girelli et al. 2000; Henik & Tzelgov 1982; Rubinsten et al. 2002; Tzelgov et al. 1992). However, recently we examined whether the factors discriminability and variability affected the size congruity effect. We found that modulating these factors does not affect the size congruity effect, even when they are completely biased toward the other dimensions in discriminability or variability, and the size congruity, in contrast to Algom's arguments, does not disappear (Cohen Kadosh et al. 2008e). Furthermore, a careful examination of Algom and colleagues' previous studies reveals that the size congruity effect disappears when only two numbers are being presented (Pansky & Algom 1999). This limited amount of stimuli increased the chance for response repetition, thus creating a confound. Cohen Kadosh, Gevers, and Notebaert (submitted a) examined this issue, and found that the size congruity effect disappears when the response sequence of the irrelevant, rather than the relevant dimension, is repeated. In light of the issues that we raised here, we disagree with Algom's theoretical perspective. Variability and discriminability play little role in the appearance of the size congruity effect, and other factors, such as response repetition (or processing speed; Cohen Kadosh et al. 2008e) that were confounded with variability and discriminability in some experiments, might diminish the size congruity effect.

Our view of automaticity, however, is compatible with **Algom**. We agree with Algom that automatic processing and intentional processing are not dichotomous, but are end-points of a fine-grained continuum, and that numerical magnitude is not activated in an automatic fashion on an unlimited scale (see also, Schwarz & Ischebeck 2003; Tzelgov & Ganor-Stern 2005).

Algom's concern from the adaptation paradigm is partly justified (as we mentioned in sect. 11). Namely, he suggests that some features of the experimental situation might encourage numerical processing, and this is totally compatible with our claims in the target article, as we suggested that the specific instructions by the experimenters might lead to different patterns of activation (see also, Piazza et al. 2007). In addition, other non-numerical factors should be controlled, as was done in other studies (Ansari et al. 2006a; Cantlon et al. 2006; Cohen Kadosh et al. 2007b), and preferably the level of activation in the parietal lobes should be modulated by numerical quantity factors (e.g., numerical deviation from the adapted quantity; Ansari et al. 2006a; Piazza et al. 2004; 2007). However, stating that a passive viewing task is a suboptimal tool to explore neuronal specialization is overstating the case. Passive viewing is just another task, and one should not use a single approach to characterize how cognitive processes are operationalized, and how the brain is organized. This seems to be a general problem that many commentators such as **Orban**; **Wiefel, Pauen, & Dueck** (**Wiefel et al.**); **Mayo**; and **Freeman & Kozma** have criticized (e.g., paradigm/technique *x* is not suitable) or praised (e.g., paradigm/technique *y* is the solution) (see sect. R6). However, we believe that integration and variety of different paradigms/techniques is the right approach to pursue, and our theory in the target article is not based on a single given paradigm/technique.

Other commentators are not convinced that intentional processing is inherently unsuitable for testing the effect of notations. We are puzzled by this position, as we showed that several studies (Cohen Kadosh 2008a; Dehaene et al. 2008; Droit-Volet et al. 2008; Ganor-Stern & Tzelgov 2008; Holloway & Ansari, 2009) used intentional numerical processing and still obtained different numerical quantity effects for different notations. To be accurate, we argued that non-intentional tasks are *more sensitive* to differences in the representations for different notations, and this is also reflected in our model (see target article, Fig. 5).

Algom also provides some experimental evidence that allegedly supports the existence of an abstract representation. However, in the discussed task, both Arabic digits and verbal numbers are presented, and the task is an intentional comparison task. We cannot understand how such a design can overcome the limitations that we mentioned in our review. Moreover, the effect of the Arabic digits on verbal numbers processing was approximately twice as large as the effect of verbal numbers on Arabic digits, although the processing time for Arabic digits and verbal numbers seems to be equal. This finding is not completely in line with the abstract view, and actually is in line with the idea of multiple numerical representations, and our model.

Finally, some authors consider parity a suitable measure for non-magnitude processing, for example, in priming tasks. Tzelgov and Ganor-Stern (2005) noted that the level of triggering (i.e., activation of the irrelevant dimension, in this case magnitude, provided by the experimental task) by numerical parity task is high. This is due to the fact that both dimensions are numerical and require semantic access to numerical information. Therefore, the processing of the relevant parity dimension can trigger the processing of the irrelevant magnitude dimension. This notion of triggering is also important to priming studies that are cited in the priming section.

Cohen argues that numerical representations are neither abstract nor automatic. We agree with the first part of the statement and, to some degree, also with the second part. Numerical representation is not always automatic (see our reply to **Algom**). Different tasks will lead to different degrees of automaticity. This relates to the notion of triggering that we mentioned in the previous paragraph. The comment made by Cohen that numerical distance is one of several features that are correlated with the order of the numbers on the number line, and that researchers rarely (if ever) consider plausible alternatives to the numerical distance hypothesis is true (for similar views see Cohen Kadosh et al. 2008b; Van Opstal et al. 2008a). For example, the numerical distance effect might be affected by linguistic frequency (Cohen Kadosh et al. 2009; Landauer & Dumais 1997). However, some studies were able to limit the number of other factors that might affect the numerical distance effect (Lyons & Ansari 2009; Tzelgov et al. 2000; Van Opstal et al. 2008b), and still observed the distance effect. We believe that numerical information can be processed automatically, but further processing is required for it to affect performance (Cohen Kadosh et al. 2008e). The results by Cohen (2009) are important, and should be examined with other paradigms, and also under conditions in which the physical shape is harder to process.

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Ganor-Stern raises important points to consider when one finds differences between notations under automatic processing, before concluding that numerical representation is not abstract. We agree with part of her comments, and considered them in previous works. For example, Cohen Kadosh et al. (2008e) found that the processing of verbal numbers differs from digits not only quantitatively, but also *qualitatively*. In addition, at least in size congruity tasks, slower access to abstract representation (see also **Grabner** and **Santens, Fias, & Verguts** [**Santens et al.**]) should have led to larger size congruity effects with the slower processed notation when it is the relevant dimension, and smaller size congruity effect when it is the irrelevant dimension (Schwarz & Ischebeck 2003), but these patterns of results were not obtained (Cohen Kadosh et al. 2008e; Ito & Hatta 2003). Therefore, speed of access to the representation cannot (fully) explain the interaction between notation and congruity. Ganor-Stern mentions that finding a size congruity for the mixed notations, as in Ganor-Stern and Tzelgov (2008), is evidence for an abstract representation. This might be the case, but a more likely explanation, in our view, is that each notation activated a separate representation and the conflict arose at the response level. This response-related explanation for the size congruity effect has support from recent studies that examined the source of the size congruity effect (Cohen Kadosh et al. 2007c; 2008d; Szűcs & Soltész 2007; Szucs et al. 2007; Szűcs et al., in press) (see also our remarks in response to **Algom**).

Even the argument that the size congruity effect is obtained not only for digits, but also for verbal numbers (although the effect is qualitatively and quantitatively different), does not indicate that numbers are represented abstractly, as size congruity is obtained also for non-numerical dimensions, for example, animals' names (Rubinsten & Henik 2002); but it will be odd to claim that animal names shared an abstract representation with digits. This type of argument demonstrates our view that similar behavioural results do not indicate shared representation. Even if one assumes that some of the parameters that **Ganor-Stern** mentioned are correct, it is not apparent why she concludes that automatic numerical processing is based on an abstract representation. We nevertheless agree with Ganor-Stern that not *any* non-additive difference between numerical processing of the different notations is evidence for a notation-specific representation, and the differences should be theoretically relevant to the issue in question. The results that we reviewed in Section 6 of the target article are in line with this view.

Núñez gave some examples from the productive side of cognition. We think that more research on the issue of the productive side in numerical cognition is required, and thank Núñez for pointing out this issue. We nevertheless think that some of the examples might not be suitable for examining automatic processing. The reason, in our view, is that they do not fit with the view of automaticity, that is, they are all task-relevant, and therefore are monitored (e.g., are parts of the conversation, and therefore deliberative; Dulany 1996).

Tzelgov & Pinhas suggest that although different populations of neurons are sensitive to difference numerical representations, at the level of brain area (horizontal IPS) numerical representation is abstract. We do not agree with this definition. The question is one of (spatial) resolution, and the better it is, the better one will be able to discriminate between different representations or other processes. For example, looking at Tel-Aviv and Jerusalem on a map with a scale of 1 : 30,000,000 cm one will not find any difference in the location of these cities; however, at a scale of 1 : 10,000,000 cm the differences between these cities are apparent. One would not conclude that at the more crude scale these cities are the same. The same logic can be applied when one needs to detect differences in the human brain.

Another issue, as **Tzelgov & Pinhas** rightly pointed out, is that single-digit positive integers may be considered as the "primitives" of numerical cognition and are automatically accessed. However, the same is also true for non-symbolic numbers (Gebuis et al. 2009; Roggeman et al. 2007), and for verbal numbers (Cohen Kadosh et al. 2008e; Dehaene & Akhavein 1995).

R2. Developmental and educational questions

The commentators raise very important issues about the construction of numerical representation over the course of learning and development. We are grateful for these comments, as they make the discussion much fuller and complete, and we dealt in our review mainly with adults and less with infants and children.

Ansari suggests that abstract representations of numerical magnitude are a more plausible outcome of development than non-abstract representations. He claims that, "while the processes that are involved in mapping from external to internal representations may differ between stimulus formats, the internal semantic referent does not differ between representation formats." We agree with the first part of his claim, but could not understand what is the evidence for the last part, that is, that the internal semantic referent does not differ between representation formats.

Ansari further suggests that format-specificity lies in the process of mapping between different external representations, and the mapping between external representation and internal numerical representation. However, this suggestion is invalid given the experimental evidence that we provided mainly in section 6. The differences are not only in general processing speed, and the parameters that reflect the numerical representation differ quantitatively and even qualitatively both for symbolic and non-symbolic numbers. Ansari also discusses the developmental trajectory for format-independent representation, which **Kucian & Kaufmann** extend and for which they provide a theoretical framework that hypothesises the creation of increased format-independent representation from format-dependent representation. Kucian & Kaufmann and Ansari might be right, and further research is needed, but we suggest that: (1) this format-independent representation is partly due to maturation of the prefrontal cortex, and (2) that it is a working representation and not the default representation (and therefore it needs a mature prefrontal cortex). The results from children and monkeys (Cantlon et al., in press; Diester &

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Nieder 2007), which have a less developed prefrontal cortex (Striedter 2005; Tsujimoto 2008), support this idea.

Another possibility that the commentators did not mention is that infants might have initial shared representation for numbers, but with learning, and interaction with the environment, there is a neuronal specialisation in the brain that leads to multiple numerical representations. This idea is feasible (Johnson 2001), and has been shown in other domains (Cohen Kadosh & Johnson 2007). For example, children do not show cortical specialisation for face processing and other non-facial objects. However, as a function of development and interaction with the environment, their brain becomes tuned to different categories (Johnson et al. 2009). We see no reason why numbers, which depend much more on education, and are acquired later in life, will not follow a similar trajectory of neuronal specialisation. (See also the comment by **Szűcs, Soltész, & Goswami** [**Szűcs et al.**].)

Ansari also bases his suggestions on the recent study by Cantlon and colleagues (Cantlon et al., in press), however, this functional magnetic resonance imaging (fMRI) study involved an intentional comparison task, and therefore has the limitations that we mentioned in section 5. Moreover, the discussed study focused only on what is shared between symbolic and non-symbolic numbers, and neglected the important question of the differences between the notations, and whether children show more evidence of the existence of non-abstract representations than adults. However, as this study suffers from the limitations that we discussed in section 5 (e.g., the insertion of response selection to the experimental task, spatial resolution), we are not sure if it is the most optimal study to shed light on this question.

An important point **Ansari** mentions is that, "If the proposal by CK&W is indeed correct, then the current models of the development of numerical magnitude representations need to be radically revised," and that "children cannot use their semantic representation of number words in order to begin understanding the meaning of Arabic digits." Therefore, this may have educational repercussions and lead to less focus on the relationships between different formats of representations in the classroom. However, cognitive psychologists have shown that humans are able to learn artificial digits to a high level of expertise, and show numerical effects, even without any connection to numerical information, symbolic or non-symbolic (Tzelgov et al. 2000). This might suggest that it is not necessary to map one numerical notation to another in order to have intact numerical understanding. Moreover, it might be that this mapping is even maladaptive. For example, children with visuospatial impairments might suffer from mapping digits to numerosity, or children with dyslexia might have similar problems if required to understand digits by mapping them to verbal numbers. At this stage, our discussion is purely theoretical, but a better understanding might be able to shed light on the connection between visuospatial impairment and dyscalculia (Rourke 1993), as well as dyslexia and dyscalculia (Rubinsten & Henik 2009).

Cantlon, Cordes, Libertus, & Brannon (**Cantlon et al.**) (see also **Núñez**) argue that the stipulation that numerical abstraction requires identical responses in identical neurons is potentially impossible to satisfy. We find this statement paradoxical, since Cantlon and colleagues stated recently that, "different quantitative dimensions can be represented by generic magnitude-coding neurons" (Cantlon et al. 2009, p. 89). For other non-numerical features in the ventral stream, it is also possible (e.g., Sawamura et al. 2006). Cantlon et al. argue that even if it is possible to satisfy this criterion (see Diester & Nieder [2007] for fulfilling this criterion for numerical representation in the prefrontal cortex), it is not clear whether it is the appropriate criterion for establishing numerical abstraction.

We would like to thank **Houdé** for his suggestion that the initial numerical representation is not abstract, and that abstract numerical representation is gained through inhibition processes. This leads to support for our suggestion that abstraction is created intentionally, but does not exist as a default representation, or, in **Tzelgov & Pinhas**'s terminology, it is a "working representation." The involvement of inhibitory operations is subserved by prefrontal cortex maturation (Tsujimoto 2008; Wood et al., in press), and therefore, the involvement of prefrontal cortex in creating an abstract representation is also in line with our dual-code model. Houdé provides important evidence that children up to the age of 7 years confuse the layout of the display with the numerical estimation. **Kucian & Kaufmann** provide another example from 3-year-old children, who seem to rely on perceptual cues if the ambiguity between numerical and non-numerical stimulus properties is overwhelming (Rousselle et al. 2004; cf. Hurewitz et al. 2006, for evidence with adults; but see Gebuis et al. 2009). **Wiefel et al.** present data on calculation tasks in toddlers showing that number operations strongly depend upon how numerosities are presented at preschool age. Elementary school education teaches the children to flexibly shift between the different numerical notations. Future studies should examine whether this shift is due to maturation of the prefrontal cortex, expertise, and education. However, these results, as well as others that were mentioned in this section, are in contrast to **Cantlon et al.**'s argument against the existence of non-abstract representations in early developmental stages.

We would like to thank **Peters & Castel** for highlighting the influence of the nature of numerical representation, whether intentional or automatic, on decision-making. Indeed, this will generate a new area of research that will elucidate the significance of numerical representation in everyday decisions. Another important comment is that, to have a better understanding of numerical representations, researchers need to examine this question in connection with individual use of numbers. Will high expertise with numbers be associated with non-abstract representation, or vice versa? We believe that this question will be of interest for cognitive psychologists and developmental psychologists.

Rosenberg-Lee, Tsang, & Menon (**Rosenberg-Lee et al.**) highlight the scenario in which various numerical notations exploit magnitude-processing capacities in the IPS to different degrees. More specifically they suggest, based on behavioural, neuroimaging, and single-cell neurophysiology studies, that at a first stage, different numerical notations are encoded in the IPS in a non- magnitude-dependent fashion. As a function of experience these non-magnitude representations become involved in automatic analogue magnitude

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representations. This is a powerful prediction, and as suggested by Rosenberg-Lee et al., future studies that will use learning paradigms and longitudinal developmental research will shed light on this developmental hypothesis. One interesting question is how different hemispheres are influenced by these developmental trajectories. Why, in Cohen Kadosh et al. (2007b), did the right IPS not show adaptation for verbal numbers (which is in line with Rosenberg-Lee et al.'s suggestion), while the left IPS did show an adaptation?

Szűcs et al. emphasize the educational perspective in numerical cognition. They make a clear distinction between an evolutionarily grounded sense of magnitude and a culturally acquired abstract number concept. They further suggest that developmental and cultural studies do not support the idea of format-independent numerical representation. They also raise another issue that is of high importance: whether numerical representation causes better math skills, and vice versa, or whether there is any correlation between these two abilities at all. We believe that further studies are needed to examine this issue, which at the moment shows more support for the connection between numerical abilities and math skills (Booth & Siegler 2008; Rubinsten & Henik 2009)

In contrast to the nativist approach that is dominant in the field of numerical cognition, **Kucian & Kaufmann** base their discussion on "neural constructivism" – which suggests that the representational features in the human neocortex are dynamic and influenced by interactions between neural growth mechanisms and environmentally derived neural activity. This view is also in line with the suggestions made by **Szűcs et al.** We are more sympathetic to this approach; numerical skills that are heavily influenced by education and environment (e.g., Hung et al. 2008; Tang et al. 2006b) will probably be modified as a function of development and training. After Kucian & Kaufmann provided evidence for non-abstract numerical representations from studies that include children with typical and atypical development, they presented a model that describes the overlap between different numerical representations as a function of age, experience, and schooling. We found this model stimulating, and it emphasizes the dichotomy in the field of development on numerical representation: **Kucian & Kaufmann**, **Wiefel et al.**, **Ansari**, and **Houdé** suggest that the numerical representation at early developmental stages is non-abstract, whereas **Cantlon et al.** suggest that the numerical representation *de novo* is abstract.

On the whole, it seems that commentators from the field of developmental psychology/neuroscience did not reach a consensus, but most of the commentators supported the existence of non-abstract representations. One should note that the computational model by Verguts and Fias (2004) assumes abstract representation by training digits and non-symbolic numbers together (thus also biases the model from the beginning toward abstract representation). In light of the comments in this section, it seems that this model should examine different methods for learning and development of numerical representations.

In sum, we are happy to trigger such a scientific disagreement and hope that future studies will shed further light on this issue.

R3. Multiple representations or multiple access?

Grabner emphasizes the importance of considering symbol-referent mapping expertise in theories of numerical representation. We agree with his suggestion, and believe that such an approach can provide better understanding of learning, education, and development, and in addition, provide knowledge on how the different representations can be created and modified as a function of symbol-referent mapping. We would like to stress that, in our case, the differences between numerical representations cannot stem from differences in the access to the numerical representation. In this scenario, one would find differences in the overall processing time and/or accuracy, but not different numerical representation-related effects for different notations (e.g., different Weber-ratio: Droit-Volet et al. 2008; mapping of number into space: Dehaene et al. 2008; distance effect: Cohen Kadosh et al. 2008e; Ganor-Stern & Tzelgov 2008; Holloway & Ansari 2009), or size congruity effect (e.g., different facilitation, interference, and differences between incongruent and congruent conditions: Cohen Kadosh et al. 2008e; Ganor-Stern & Tzelgov 2008; Ito & Hatta 2003). Moreover, in some cases, even when the differences in the processing time between the different notations is taken into account, this cannot explain the differential effects for different notations (e.g., Cohen Kadosh et al. 2008e). Lastly, the difference in symbol-referent mapping expertise cannot explain why, in brain imaging studies, left or right IPS is notation-sensitive, while the contralateral IPS does not reach significance (Cohen Kadosh et al. 2007b; Piazza et al. 2007).

Another argument by **Cantlon et al.** is that the observed interactions are due to some ceiling or floor effects for one dimension but not the other. This might apply to a small fraction of the studies that we presented (e.g., Dehaene & Akhavein 1995), but cannot explain other results. The interactions between different formats and factors that originate from the mental number line include different Weber-ratios for different modalities (Droit-Volet et al. 2008), different mappings of different numerical formats on a physical line (Dehaene et al. 2008), or correlations between math abilities and performance in one numerical format, but not another format. These are all instances of evidence of non-abstract representations that are not due to floor or ceiling effects. The same holds also for the neurobiological evidence that we provided, and especially the case of double dissociation (sect. 6).

Furthermore, the argument that the classification by Dehaene et al. (1999) for *approximate* and *exact* can explain our results, is not accurate. Although, we agree that there is overlap between our model and the approximate–exact numerical codes, which we originally mentioned in section 10, our model has more explanatory power. For example, our model presents a continuum rather than a binary classification to approximate and exact systems that are subserved by different brain areas. In addition, our model explains the classification between different symbolic notations, and not only between symbolic and non-symbolic notations.

Dehaene's rebuttal of the non-abstract view dismisses some of the data that we provided – which found differences between a variety of numerical formats in different

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paradigms, labs, and techniques – by calling them "weak evidence." Dehaene's description of the data from behavioural, neuroimaging, transcranial magnetic stimulation (TMS), and single-cell neurophysiology that showed evidence for multiple numerical representations as "occasional" also avoids serious discussion. Dehaene states that our review of findings (which he terms a "catalogue") of difference or interaction involving number notations in support for the notation-specific view is wrong. However, looking at previous studies by Dehaene on this question shows that he bases his argument toward the abstract view by not finding differences between notation, or an interaction (Dehaene 1996; Dehaene & Akhavein 1995; Dehaene et al. 1998a; 2003).

Dehaene also discusses the single-cell neurophysiology results from the prefrontal cortex, while not considering the results in the IPS that were observed in the same study (Diester & Nieder 2007). We are said to dismiss these results. However, we focus in our target article on the IPS, the key area for numerical cognition, which is highlighted by Dehaene in many papers (Dehaene et al. 1998a; 2003; 2004). It may be that Dehaene is revising his position, and now suggests that numerical abstraction is in the prefrontal cortex, rather than the parietal cortex. However, before this conclusion can be reached one has to take into account that these data were: (1) obtained after explicit training of associating digits with numerosity (e.g., 1 is one dot), and (2) in intentional task. Both of these factors might have contributed to the results that were obtained in the prefrontal cortex, as we discussed in the target article.

Dehaene also gives some new unpublished data from his lab (i.e., Eger et al., submitted). It is clear from his description that the task was intentional, and we stressed in our article the limitations of using such tasks. On the other hand, it is unclear if response selection was required in this study, and moreover, the IPS decoder is still limited to the voxel level; and therefore Dehaene ignores our comment that not finding a difference between the notations does not imply that there is an abstract representation: absence of evidence is not evidence of absence; a single demonstration of a dissociation is more compelling than a failure to find evidence of segregation. Nevertheless, if one would like to seriously consider these results as indicative of abstract representation, there are two further analyses that we suggest Eger, Dehaene, and colleagues conduct: First, to show also that when trained with dots, the IPS decoder generalised to digits. Second, to examine the existence of segregation in the multivoxels pattern by using multivariate pattern analysis. Accordingly, in a recent fMR-adaptation paradigm in which subjects processed the colour of the stimuli, we found that that the numerical representation for digits and dots is subserved by overlapping multiple representations that are format-dependent (Cohen Kadosh et al. 2008a). One of the analyses that support such a view is a multivariate pattern analysis. If we are right, and indeed the task that **Dehaene** reported is intentional, this provides strong support for the model that we presented in section 10. Other evidence is offered showing that the classifier trained with the posterior IPS activation during saccades could be generalised to a classification of subtraction versus additional trials independent of the notation (digits, or dots) (Knops et al., in press). Reading this work reveals that the activation that Dehaene mentions was found in the bilateral posterior superior parietal lobule (PSPL), an area that according to him and others is outside the classical areas that are involved in numerical representation per se (Cohen Kadosh et al. 2008f; Dehaene et al. 2003). Moreover, in previous works Dehaene and others considered the PSPL as involved in attention, orienting in space, and attentional selection, rather than numerical representation per se (Dehaene et al. 2003). Surprisingly, the horizontal IPS (hIPS) that has been found to be involved in numerical representation in meta-analyses by us (Cohen Kadosh et al. 2008f) and by Dehaene and colleagues (Dehaene et al. 2003), did not show a shared decoding for numerosity and digits. This point supports the idea that the shared coding for numerosity and digits did not occur at the level of the representation.

We found **Dehaene**'s contention that the PSPL is a "cortical recycling" of a *sensorimotor* area for a more abstract mathematical use puzzling. This is a new argument that does not appear to be consistent with his previous position that the horizontal segment of the IPS (hIPS) is the area that is involved in abstract numerical representation and calculation (Dehaene et al. 2003; 2004), and the putative area for the cortical recycling seems to fall out of the PSPL (see Figure 2 in Dehaene & Cohen 2007). Indeed, in a meta-analysis the hIPS was found by Dehaene et al. (2003) to be involved in abstract mathematical use. As Dehaene puts it: "Those parametric studies are all consistent with the hypothesis that the HIPS codes the abstract quantity meaning of numbers rather the numerical symbols themselves" (p. 492). In a more recent meta-analysis of numerical cognition (Cohen Kadosh et al. 2008f) we found that the middle IPS is involved in numerical representation. In a comprehensive review of the literature, Dehaene identified the PSPL as "being involved in attention orienting in space, can also contribute to attentional selection on other mental dimensions that are analogous to space, such as time, space, or number" (Dehaene et al. 2003, p. 498). The differences in the coordinates of the PSPL and hIPS are too large to be ignored (more than 2 cm on the anterior to posterior axis) (hIPS: $x = 41$, $y = -47$, $z = 48$ [Dehaene et al. 2003]; mIPS: $x = 37$, $y = -46$, $z = 42$ [Cohen Kadosh et al. 2008f]), and PSPL: $x = 32$, $y = -68$, $z = 46$ [Sereno et al. 2001). Moreover, the behavioural part (Knops et al. 2009) of the cited work is based on several important differences between symbolic and non-symbolic notations that are in line with **Campbell & Metcalfe**'s view. This part was not considered by Dehaene.

Dehaene ignores other results that are not in line with the abstract view. For example, he claims that notation effects "occasionally" affect performance because of numerical precision. Numerical imprecision is observed with non-symbolic numbers (Izard & Dehaene 2008). However, this cannot explain the differential effects between symbolic notations (Arabic digits, Indian digits, Kana, Kanji, verbal numbers in different language), which others, including Dehaene, have observed (see sect. 6 of the target article). Another invalid argument is that the effects – for example, between digits and verbal numbers – are due to speed of processing and perception, or occur at the transcoding level. However, these factors were taken into account in previous studies (e.g., Cohen

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Kadosh et al. 2008e), and again some effects that we mentioned cannot be explained by these factors (e.g., Cohen Kadosh et al. 2007b; Dehaene et al. 2008; Droit-Volet et al. 2008; Holloway & Ansari 2009). It is ironic that this comment is made by Dehaene, who based the abstract numerical theory partly on null differences between digits and verbal numbers (Dehaene 1996; Dehaene & Akhavein 1995). If the effects in the studies that we mentioned are due to speed of processing, or are perceptual, or occur at the transcoding level, then his earlier results should have being interpreted as evidence toward the non-abstract view.

Dehaene concludes that considerable evidence points to a notation-independent representation in the monkey IPS. We ask which evidence? The only evidence is for notation-dependent representation in the monkey IPS (Diester & Nieder 2007; see section 8 of the target article and Fig. 4).

We agree with **Dehaene** that the IPS in humans and monkeys is not a module for representation, and it includes highly distributed neurons in the IPS that are intermingled with other representations of time, space, and other continuous dimensions, including numbers as proposed by Walsh (Walsh 2003), and has been tested and confirmed later by others (Cohen Kadosh et al. 2005; Pinel et al. 2004; Tudusciuc & Nieder 2007; for a review and meta-analysis, see Cohen Kadosh et al. 2008f). We do not see any reason why the principles of these distributed magnitude neurons should not be extended also for different numerical notations.

Santens et al. suggest that the differences between notations in behavioural and neuroimaing studies can occur because of some divergence between the input pathways to this common representation. One should notice that the model by Verguts and Fias (2004) does not include any different pathways for different symbolic numbers, but only differentiates between symbolic and non-symbolic numbers. Moreover, none of the models (including Verguts & Fias 2004) can explain the interaction between effects that stem from numerical representation and different symbols for numbers. Therefore, we do not see any support for Santens et al.'s suggestions, even from their own studies (Santens et al., in press) and model (Verguts & Fias 2004).

Some commentators argued that the effects we discussed might occur prior to the level of numerical quantity representation. Therefore, some clarification is needed. We did not intend to challenge the idea that number words and digits are processed differently at the perceptual stage – and it would be wrong to do so, since there are many studies that showed this difference in processing, including Dehaene (1996) and Schwarz and Ischebeck (2000). Therefore, we did not base our conclusions on the overall difference in reaction times (RTs) between number words and digits, which stems also from differences at the perceptual stage. Rather, the crucial point is the interaction between notation and effects that are post-perceptual and stem from the level of the numerical representation or even later. For example, many studies have shown that the distance effect is independent of the perceptual stage since it takes place at a post-perceptual stage, whether at the level of numerical representation (e.g., Barth et al. 2003; Cohen Kadosh et al. 2007c; Dehaene 1996; Pinel et al. 2001; Schwarz & Ischebeck 2000) or response selection (Cohen Kadosh et al. 2008b; Link 1990; Van Opstal et al. 2008a; Verguts & Fias 2004). Note that in the case of an interaction between distance effect and notation, it does not matter whether the locus of the distance effect is at the level of numerical representation or response selection, because response selection follows the level of the numerical representation. All studies that examined the differences between notations involved different visual displays for their notations, and there were differences in the overall RTs. However, the distance effect is the key effect for examining the question of abstract numerical representation because it taps post-perceptual stages (as reflected by event-related potential (ERP) (e.g., Dehaene 1996; Libertus et al. 2007; Pinel et al. 2001), fMRI (e.g., Eger et al. 2003; Pinel et al. 2001), and behavioural results, which have been shown specifically and convincingly by the sequential paradigm (Cohen Kadosh 2008a; Schwarz & Ischebeck 2000). Another piece of evidence is that in ERP studies, the number of letters (but not the distance effect) modulates the N1 component (perceptual component) (Dehaene 1996). However, the distance effect affects only later post-perceptual components (P300: Cohen Kadosh et al. 2007c; Schwarz & Heinze1998; P2p: Dehaene 1996). In addition, we are not familiar with any findings in the neuroimaging literature (or any other method) that have shown modulation of the perceptual areas by numerical distance and notation when words and digits were used (e.g., Pinel et al. 2001).

Falter, Noreika, Kiverstein, & Mölder (**Falter et al.**) support the non-abstract view for numerical representation, and extend it to other domains such as time. They show that not only numbers are represented non-abstractly, but also other representations that involve the IPS, such as time. In our view, this idea should generate further experiments that will examine the representation of time, similar to our suggestions for numbers.

Campbell & Metcalfe support our theoretical view, and extend it to basic arithmetic. They provide evidence that basic arithmetic is not abstract in two ways. First, it is based on discrete, format- and operation-specific processes. Second, calculation efficiency is format-specific. Our view is very close, and indeed, Campbell was one of the few who has supported the idea of non-abstract numerical representation in the last 20 years (Campbell 1994; Campbell & Clark 1988; Campbell & Epp 2004; 2005). Moreover, our view that strategies might play a role in numerical representation is similar to his view that arithmetic is affected by subjective strategies. We believe that future studies should examine the issue of strategies on numerical representations, as it will clarify why some labs reveal non-abstract representations while others do not find any differences between the different formats. We need to take into account what exactly the researcher tells the subject. This has been shown to affect the results in some studies that reported these instructions (Piazza et al. 2004; 2007).

R4. Priming

Part of the evidence that **Dehaene**, **Reynvoet & Notebaert**, and **Santens et al.** focus on is subliminal priming. Surprisingly, they all ignore the good evidence that subliminal priming can originate at the level of response (for behavioural evidence, see Kiesel et al. 2007; Kunde et al. 2003; 2005; for fMRI and ERP

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evidence, see Dehaene et al. 1998b). More surprising is that Dehaene uses the cross-notation subliminal priming data from Naccache and Dehaene (2001a) in his commentary (see Dehaene's Fig. 1) to argue that digits and verbal numbers have a shared representation. However, these data are based on the same data in earlier work by Dehaene et al. (1998b). In this work, Dehaene et al. showed that an unconscious prime (digit or verbal number) is processed up to the response level (see Figs. 3 & 5 in Dehaene et al. 1998b). Therefore, the results by Naccache and Dehaene (2001a) can be explained perfectly by response selection rather than shared numerical representation, which is in line with other behavioural evidence in the field of subliminal priming (Kiesel et al. 2007; Kunde et al. 2003; 2005). Therefore, both digits and verbal numbers were processed up to the response level, a result that is in line with the non-abstract view (e.g., the digit 1 activated response by the left hand and the verbal number NINE activated response by the right hand), and can explain the subliminal priming effect (Kiesel et al. 2007; Kunde et al. 2003; 2005). Support for our view also comes from another study that used functional connectivity analysis. It was shown that the IPS and the frontal eye field, that are involved in response selection, are also coactivated with the motor cortex, when numerical magnitude is processed up to the response level (Cohen Kadosh et al. 2008d). Therefore the activation in the IPS in Naccache and Dehaene (2001a) and the motor cortex activation in Dehaene et al. (1998b) that were observed in the same data, can be argued to be functionally connected and involved in response selection, rather than shared representation.

Another issue is that some of the results from the cited subliminal priming studies actually support the non-abstract view, for example, by suggesting a preferred format to which the different numbers are mapped (e.g., digit; Noël & Seron 1993). Unfortunately, alternative explanations are given to explain these effects that are not compatible with the abstract view, rather than mentioning the additional support for the non-abstract view (see, e.g., **Santens et al.**).

Reynvoet & Notebaert also raised the issue that some of the evidence in favor of a notation dependent magnitude representation is based on a null effect in a particular condition. It is true that in some results a null effect was observed for one notation and not for another, but this is only a small fraction of the data, and other studies show that the numerical representation depends on the notation both qualitatively and/or quantitatively (e.g., Cohen Kadosh et al. 2007b; Cohen Kadosh et al. 2008e; Dehaene et al. 2008; Droit-Volet et al. 2008; Ganor-Stern & Tzelgov 2008; Holloway & Ansari 2009; Nuerk et al. 2002; Piazza et al. 2007).

The researchers who are working on priming suggested that subliminal priming is automatic. However, they would need to take into account the view that the priming distance effect is not evidence for automatic processing, but rather of incidental processing (Tzelgov & Ganor-Stern 2005).

R5. Terminology

Several commentators raised the issue of the definition of abstract. We based our review on a previous and well-accepted definition in the field of numerical cognition, and we are grateful for their contributions that will provide us with a better definition for the abstract representation.

Núñez criticizes our characterization of abstraction. He mentioned that this definition is specific and unnecessarily restrictive, thus making the extension to other non-numerical areas of cognition hard. We are sympathetic to this concern, but see no reason why the terminology of abstract in the field of numerical cognition cannot be applied to other domains. It is interesting to note that numbers as a concept do not clearly fall into abstract or concrete categories. For example, *chair* is more concrete than *truth* but 2 does not fall clearly into one of these categories, and can vary among these dichotomies.

Pease, Smaill, & Guhe (**Pease et al.**) also comment on the definition of abstraction in the field. We agree with their view that a binary distinction between abstract and non-abstract is not the optimal way to conceptualise the problem, and our model reflects this view. Pease et al. suggest also that multi-modal representations of mathematics, such as diagrammatic or algebraic reasoning, are assumed to abstract to a common domain. We do not agree with this claim, and several researchers argued that the deeper knowledge of experts facilitates the ability to integrate the different representational formats (Ainsworth et al. 2002; Kozma et al. 2000; Tabachneck et al. 1994) (see **Peters & Castel**, for some support with this view in numerical cognition). This idea is similar to the one made by Lakoff (2008) that Pease et al. cite, and is similar to our suggestion, that the numerical representation is composed from multiple representations, and that a strong association can be created between them by the subject as a working representation.

Piazza & Izard raise many questions that will be of interest for future studies. We agree with them that abstract representation has become the default theory of the mathematical brain; indeed the need for our target article is partly predicated on the fact that it has become an unhealthily unquestioned default. However, in contrast to their claim, we do not offer a dichotomy (see Fig. 5), and our focus on non-abstract representations was done in order to shake the foundations of the prevailing orthodoxy, which leading researchers have ignored to some degree (Piazza & Dehaene 2004; Piazza et al. 2007; Pica et al. 2004).

In contrast to **Piazza & Izard**'s claims, we also do not view numerical representation as a module, and we stated in our review our divergence from such a view (see sect. 5). Neuronal populations that code numerical quantity can be modality-sensitive, but they can still be sensitive to other non-numerical features. As for the issue of serial processing: albeit that there is ample evidence that supports the idea that numbers are processed serially (Blankenberger & Vorberg 1997; Dehaene 1996; Schwarz & Ischebeck 2000), the interaction between modality and numerical effects, such as the distance effect, does not depend only on serial processing, because the additive factor method analysis is also valid in most of the cases of cascade processing (Sanders 1998).

It is worrying that researchers in the field of numerical cognition, such as **Piazza & Izard** and **Santens et al.**, consider interactions between modality and the representation-related effects as an indication of abstract

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representation. We have explained in this section, and in section R3, why this view is wrong. Nevertheless, these commentators' view is a new view, but a risky one. If additive *or* interactive effects indicate abstract representation, the abstract view is immune to falsification – the death knell for any scientific idea.

We like very much the idea of selectivity of neurons to numbers and other features, a view that is partly in line with previous works by us (Cohen Kadosh et al. 2008f; Walsh 2003). **Piazza & Izard** gave an example of how when one examines single neuron spiking activity or the fMRI signal, some neurons that respond both to number and length, or number and motion, or length and motion, will not show selectivity when averaged across populations. Extrapolating their idea, the same can also hold when one examines dots and digits, digits and verbal numbers, and dots and verbal numbers. Given that all the studies so far were confined to only two modalities, the chance that abstract representation was concluded mistakenly is increased.

Vallar & Girelli pointed out that the dichotomy between abstract and non-abstract is too general to capture the variety of possible supramodal numerical representations. We agree with their argument, and would like to stress that our view is not that there is a dichotomy between abstract and non-abstract, but that both are endpoints of a continuum, and may interact with spatial codes. However, we believe that spatial codes do not affect different numerical notations to the same extent (see Dehaene et al. 2008, for support for our view), and therefore, that spatial codes are notation-dependent.

Pesenti & Andres raise very important points as to the definitions of abstract and non-abstract representations that are used by many authors in the field, including us. These definitions prevail also in the current issue (e.g., our target article review, the commentaries by **Dehaene**, **Cantlon et al.**, etc.). Some of Pesenti & Andres' comments are thought-provoking, such as that analog representations cannot be abstract. We are grateful for their comments, and agree that the researchers in the field of numerical cognition need to use more accurate definitions. However, we believe that their commentary raises more concerns for the existence of abstract representation. It seems that differential effects at the semantic level as a function of notation (e.g., Dehaene et al. 2008; Diester & Nieder 2007; Droit-Volet et al. 2008; Tudusciuc & Nieder 2007) cannot be compatible with abstract representation, whereas results that support the existence of shared representation do not necessarily indicate abstract numerical representation. Nevertheless, even if one abandons the definition of abstract/non-abstract representations and adopts instead the idea of shared/multiple representations, or alternatively, modality-(in)dependence, the weight of evidence seems to support the existence of multiple representations (or modality-dependence).

R6. Methodological advances

Freeman & Kozma, **Mayo**, and **Orban** offer several suggestions to advance our understanding of numerical cognition in humans and nonhuman primates.

Freeman & Kozma suggest that aside from single-cell neurophysiology, and fMRI, additional techniques such as electroencephalography (EEG) or magnetoencephalography (MEG) are required to examine the nature of numerical representations, and that these techniques will enable one to uncover the involvement of wide regions in intermittent spatially coherent oscillations. We entirely agree with their suggestions and mentioned some of them toward the end of our article.

Mayo suggests two manipulations in single-neuron recording: reversible inactivation and adaptation of apparent numerosity. We agree that these new manipulations, which to date have not been used in this context, will be of help and can provide a causal understanding of the neuronal basis of numerical processing. It is worth asking, however, whether in principal this could be established in neurons in the rat brain that responded to numerosity, or by using TMS adaptation techniques in humans.

Orban suggests that monkey fMRI provides a solution to the limitations of neuroimaging studies that we raised (which, according to him, we grossly underestimated). He correctly mentions the study by Sirotin and Das (2009) – which appeared after our target article had been accepted – to stress the idea that, compared to intentional tasks, passive tasks (e.g., adaptation paradigm) provided a better link between the haemodynamic response and neuronal activity. Indeed, adaptation paradigms have some limitations, but this is clearly a better tool to explore the theoretical question at hand, as also implied by Orban. Orban further mentions the important study by Sawamura et al. (2006) (also cited in our review), which shows that cross-format adaptation (e.g., adaptation for two consecutive trials for pigs, or hammers, vs. pig follows a hammer or vice versa) overestimates neuronal response selectivity. This point should be taken into account when the conclusions toward abstract/non-abstract are based on the level of cross-notational adaptation. After mentioning several possible methodological problems, Orban suggests the use of fMRI in the awake monkey as the solution to the theoretical question. We would suggest a note of caution in using monkeys as a model for *human* numerical cognition. Human numerical cognition cannot be studied independently of language (Carey 2004; see also **Ansari**). We must also take into account the large hemispheric asymmetries in different numerical functions, as well as deal with the human tendency to represent numbers spatially. Monkeys do not speak, do not show our pronounced lateralisation, do not represent numbers from left to right, or right to left, as far as we know, and they do not learn about numbers and quantity in the same way as humans. Technical muscle may therefore not be the answer to these conceptual questions.

R7. Simulated cognition and numerical cognition

Lindemann, Rueschemeyer, & Bekkering (**Lindemann et al.**) provide a new point of view on numerical cognition, by suggesting an action-based number semantics to provide new insights into the way that we represent numerical magnitude. They suggest that abstract representation might emerge from association between the numerical information and action. We agree with this view, which is in line with Walsh (2003), and is in

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accordance with our suggestion in the target article (i.e., abstraction requires intention).

Similarly, **Myachykov, Platenburg, & Fischer** (**Myachykov et al.**) extend our theory to the simulated cognition framework. We appreciate their innovative thinking, which suggests that understanding non-abstract representations within the framework of simulated cognition provides a theoretical platform for real-life numerical representation. Their view provides a hierarchy of features of numerical representation, which includes embodied, grounded, and situated cognition, and can explain effects in the field of numerical cognition, and provide support for some of the effects that we discussed and for our theoretical view. Furthermore, Myachykov, et al. provide the first independent experimental data to examine our dual-code model (sect. 10).

R8. Conclusions

We are grateful to the commentators for their valuable comments that helped us to refine and clarify our theoretical perspective. We have shown that even if one takes into account factors that might affect numerical representation, numerical representation is primarily non-abstract. Many questions were raised by the commentators and we are sure that new questions will come from this interaction. It is now time to return to the lab and generate new data on the ways that humans represent numbers.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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