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# Basic Number Representation and Beyond: Neuroimaging and Computational Modeling

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The Oxford Handbook of Numerical Cognition *(Forthcoming)*
*Edited by Roi Cohen Kadosh and Ann Dowker*

Online Publication Date: Jan 2015
Subject: Psychology, Cognitive Neuroscience
DOI: 10.1093/oxfordhb/9780199642342.013.68

## Abstract and Keywords

We discuss recent computational network models of elementary number processing. One key issue to emerge from this work is a crucial distinction between symbolic and non-symbolic number representation, and the related distinction between number-selective and number-sensitive coding. Empirical predictions from the models were tested, and are here summarized. Another issue is the relation with task-based decision making mechanisms. In both lab and real-life settings, representations are seldomly accessed in a task-neutral manner, rather subjects are usually presented with a task. A related theme is the functional association between number representations and working memory. In these issues also, both modeling and neuroimaging work is summarized. To conclude, we propose that the combined modeling-neuroimaging approach should be extended to tackle more complex questions about number processing (e.g. fractions, development, dyscalculia).

Keywords: numerical cognition, computational modeling, functional neuroimaging, number networks, working memory

### 1. Introduction: Number in the human and animal brain

Early in the morning, we open our eyes, and read off the time on our alarm clock. Late in the evening, we go to sleep, perhaps counting how many nights are left before the holidays. On both occasions, and many occasions in between, we are confronted with numbers. Numbers allow calculation, ordering and planning ahead, and the ability to work with numbers is considered one of the principal accomplishments of humanity.

Nevertheless, the ability to process numerical quantities in a non-symbolic format is shared with many animal species (e.g. Cantlon and Brannon 2006; Hubbard et al. 2005). Carefully controlled experiments have shown repeatedly that many animal species can indeed represent number in an abstract way (e.g. Brannon 2006). Human infants have likewise been shown to possess numerical abilities long before language develops (Feigenson et al. 2002; Xu and Spelke 2000; Xu et al. 2005). Remarkably, many properties emerge consistently across species, when humans and animals are engaged in numerical tasks (Dehaene et al. 1998; Roitman et al. 2007; Whalen et al. 1999). Two of these omnipresent properties are the distance and the size effect. The distance effect refers to the observation that it is easier to discriminate between two numbers as the numerical distance between them increases (e.g. sets of two and nine dots are easier to discriminate than sets of eight and nine dots; Moyer and Landauer 1967). The size effect refers to the observation that for an equal numerical distance, small numbers are easier to discriminate than large numbers (e.g. sets of two and three are easier to discriminate than sets of eight and nine). The distance and size effects appear in humans when numbers are presented as Arabic digits (Dehaene et al. 1990), as verbal number words (Koechlin et al. 1999) and as non-symbolic numerosities (patterns of dots) (Buckley and Gillman 1974, see also Gebuis and Reynvoet, this volume). This close correspondence between humans and non-human animals suggests that we share common structures for number processing

(Feigenson et al. 2004), the characteristics of which have now begun to become uncovered.

The first neural findings describing how number is processed in the brain were provided by Nieder and colleagues (Nieder et al. 2002; Nieder and Miller 2004). These authors trained macaque monkeys to perform a delayed match-to-numerosity task. The monkeys were presented with two consecutive dot patterns, each containing one to five dots, and were asked to indicate if the second display contained the same number of dots as the first one. Other features in the displays such as individual dot size and spatial configuration were varied randomly. The authors recorded the neuronal activity of single cells during both the sample and the test phase. They observed neurons in the prefrontal cortex and intraparietal sulcus that are tuned to numerosity: The neuronal response is maximal when that neuron’s preferred quantity is presented, and decreases systematically when the presented number of dots is numerically more distant from the preferred numerosity (cf. number-selective code in Figure 1). Hence, these neurons were called number-selective neurons. When the number of dots presented is not the neuron’s preferred quantity, but numerically close, the neuron still responds, albeit at less than maximum. Hence, neuronal activity shows overlap for two numerosities. This overlap is larger for two numerosities with a small numerical distance, making it harder to discriminate between these numerosities. For two numerosities with a large numerical distance, there is little neural overlap, making discrimination easier. In this way, the tuning properties of number-selective neurons can explain the distance effect in the match-to-numerosity task. Nieder and colleagues also observed that the tuning curves of the number-selective neurons broaden as number increases (Nieder et al. 2002). Consequently, larger numerosities are more coarsely represented and thus harder to discriminate, generating a size effect.

Also in humans, there is evidence for a number-selective coding system. In behavioral experiments, Reynvoet and colleagues (e.g. Reynvoet and Brysbaert 2004; Reynvoet et al. 2002) presented two consecutive numbers in each trial, but only the second stimulus (the target) had to be named. By varying the numerical distance between the first stimulus (the prime) and the target, the influence of the prime on target processing was investigated. The priming effects were distance-dependent, meaning that the target is named faster when the numerical distance between the prime and the target is small. This can be explained by number-selective coding: when the prime activates a number in a number-selective system, neurons that prefer numbers close to the prime number will also be somewhat pre-activated by the prime (cf. number-selective code in Figure 1), thereby facilitating the naming of a subsequent numerically close target.

Neural evidence for number-selective neurons in humans has been found using the fMRI adaptation paradigm. This method is based on the fact that, when the same visual stimulus is repeated, the activity of neurons responsive to this stimulus is reduced. Therefore, the activity of number-selective neurons responsive for a specific quantity should decrease when this quantity is repeatedly presented. This is known as adaptation of the neuronal response. Piazza et al. (2004) performed an fMRI adaptation study in which they showed adaptation of the neuronal response in the anterior part of the intraparietal sulcus after repeated presentation of the same numerosity. The response recovered from adaptation when a different numerosity was occasionally presented, but not when the same numerosity was shown with different shapes, consistent with adaptation of number-selective neurons. Moreover, Piazza et al. (2004) showed that the recovery of the response was larger for numerosities with a large distance from the adapted numerosity than for numerosities with a small distance from the adapted numerosity. This provides evidence for an activation profile of the underlying quantity neurons in terms of number-selective coding. Indeed, the response profile of this coding scheme predicts that neighboring numbers will also be activated, and thus also adapted. By plotting the recovery of the BOLD signal as a function of the presented numerosity, the authors obtained tuning curves similar to those obtained by Nieder et al. (2002). Like the tuning curves obtained with single-unit recording in monkeys, the tuning curves obtained with fMRI adaptation in humans were also broader with increasing numerosity.

## 2. Model: Number-sensitive and number-selective coding

The characteristics of the number-selective neurons account for many aspects of behavior (Nieder and Miller 2004). The question remains, however, how visual input is converted into a number-selective coding system. This conversion is most challenging for the transformation from a non-symbolic number, which consists of a number of objects (Figure 1). In an attempt to confront this issue, the systems required for this conversion have been investigated by computational modeling (Dehaene and Changeux 1993; Verguts and Fias 2004).

The models start with the representation of the visual input (i.e. a set of objects) on an object location map (see Figure 1). An object location map is a spatial neuronal map in which each neuron responds to a specific location. If an object is presented at this location, the neuron detects it and is activated, independent of the size or other visual properties of the object (Goldberg et al. 2002). Rather than being specifically devoted to number processing, this map has a more general function (e.g. supporting visuo-spatial short-term memory, Awh and Jonides 2001; Srimal and Curtis 2008; Roggeman et al. 2010). This map is already a highly abstracted transformation of primary visual cortex, because it has to generalize across different sizes and shapes of the physical appearance of individual objects (e.g. Dehaene and Changeux 1993). These visual transformation processes are beyond the scope of the current discussion. As a result of these processes, each object is represented as ‘one’ by only one location neuron.

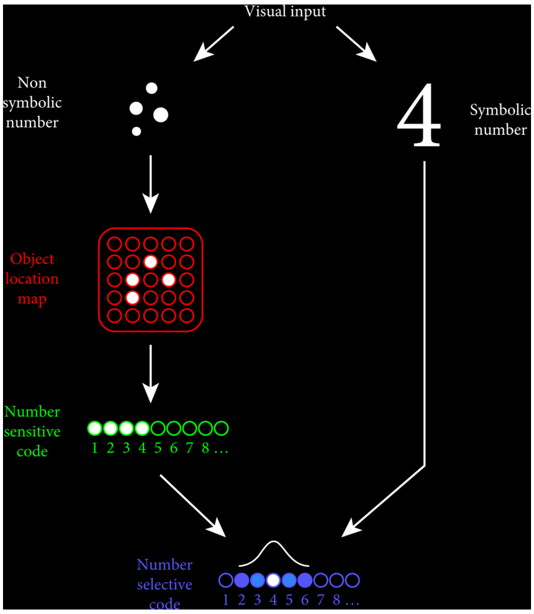

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*Figure 1* : Illustration of the pathway for the processing of number from visual input to a number-selective code. Left: processing pathway for non-symbolic number; the non-symbolic numerosity is represented in an object location map, which is transformed to a number-sensitive code (the hidden layer in our model). Number-sensitive coding is then transformed to a number-selective code to yield the final representation. Right: no nonlinearity is involved in the transformation from symbols to number-selective neurons, hence symbolic input is directly connected to the number-selective neurons.

The information in the object location map must then be converted into a number-selective code. For example, the number neuron coding for ‘1’, should be activated if only one object is presented in the object location map; the neuron coding for ‘2’ should be activated if two objects are present in the object location map, and so on. However, because objects are not always presented in the same spatial configuration, a direct transformation from the neurons in the object location map to the number-selective neurons is not possible. The reason for this is that an activated object location neuron should (for example) activate the number 3 neuron, only if exactly two other neurons in the object location map are activated. Unfortunately, the neuron in the object location map has no way of knowing this. It does not know how many other objects are represented, and hence cannot know whether to activate the number 3 neuron or another number neuron. Technically, this corresponds to an instance of the XOR (exclusive OR) rule in logic (Minsky and Papert 1969). These problems require a nonlinear transformation, which cannot be achieved in a single step. The most straightforward way to solve this problem is to implement an intermediate processing step, where the object location map information from different object location neurons can be combined. Therefore, a hidden layer was introduced in the models between the object location map and the number-selective coding system.

Verguts and Fias (2004) trained a neural network with an object location map as input. The network was trained with backpropagation to transform the object location representation of the numerosity at input via the hidden layer to a number-selective coding representation at output. Because of the backpropagation training algorithm, the network was allowed to come up with the computationally optimal solution. After training, it was found that the neurons in the hidden layer displayed a monotonically varying activation pattern (i.e. monotonously increasing or decreasing) when more objects were presented. Hence, the intermediate step between the object location map and the number-selective coding system consisted of neurons accumulating (in a positive or negative way) the number of objects that was presented at input. In other words, the neurons were sensitive to number but, importantly, were not number-selective, since they did not selectively respond to a specific number (cf. number-sensitive code in Figure 1). This way of representing number is known as number-sensitive (in contrast to number-selective). This model demonstrates that number-sensitive coding is a biologically plausible way of solving the (generalized) XOR problem implied in mapping from an object location map to number-selective coding.

Number-sensitive coding also emerged spontaneously from visual input in an unsupervised model by Stoianov and Zorzi (2012). Rather than normalize object size, these authors presented (unnormalized) visual input representing visual scenes with different numbers of objects to a so-called deep network model (Hinton 2007). The visual layer projected to a first hidden layer, which projected to a second hidden layer. Crucially, the model training was unsupervised, being required only to reconstruct the visual layer activation based on the hidden layer activation. After training, neurons in the first hidden layer were sensitive to various visual properties. Crucially, the second hidden layer contained a subset of neurons that responded more strongly (or more weakly) to larger numbers of objects (similar to the number-sensitive code in Figure 1), but were not sensitive to total area. In this sense, such neurons can be labeled number-sensitive.

In summary, a number-sensitive coding system may be a necessary preceding step in the transformation from a non-symbolic number to an abstract number-selective representation. The models thus suggested that the cardinality of a set of objects is represented differently in different stages of the processing stream: visual input is first transformed into an object location map, which activates a number-sensitive coding system, which subsequently generates a number-selective code (see Figure 1).

## 3. Data: Number-sensitive and number-selective coding

The evidence for number-selective coding was discussed in the introduction. Inspired by the computational models, researchers have recently started to look for evidence for number-sensitive coding too.

### 3.1. Single-unit evidence in the monkey

The biological reality of number-sensitive coding was demonstrated by means of single-unit recording. Roitman et al. (2007) recorded neurons in the lateral intraparietal area (LIP) of the macaque monkey. The monkeys were asked to plan an eye movement to a target. At the same time, visual arrays of 2, 4, 8, 16, or 32 dots were displayed at a distal location from the eye-movement target. The numerosity of the array predicted the amount of reward the monkey would receive when he performed the eye movement, but was task-irrelevant otherwise. Activity was recorded from neurons having the distal location of the numerical display in their receptive field. More than half of the neurons recorded in LIP displayed a monotonic response to the numerosity of the numerical arrays: the activity increased or decreased monotonically with increasing numerosity, indicating that these neurons summated (in a positive or negative way) the number of elements displayed. This finding supports the existence of number-sensitive coding in the monkey brain.

### 3.2. Behavioral evidence in humans

In humans, support for number-sensitive coding was found in a priming study by Roggeman et al. (2007). Here, the effect of a briefly presented prime on the naming of a subsequently presented target number was evaluated. Both primes and targets could be either symbolic (Arabic digits) or non-symbolic (dot patterns) number stimuli. When primes were symbolic stimuli, naming times increased with increasing distance between prime and target. This is the distance-dependent priming effect (see Reynvoet et al. 2002) reported above. In contrast, when primes were non-symbolic stimuli, naming the target value was faster whenever the value of the prime was larger than or equal to the value of the target. This step-like priming pattern is consistent with number-sensitive coding. Because large numbers lead to more activation in number-sensitive coding, a prime that is larger than the target will activate the representation of the target, facilitating the naming of the target. If the prime is smaller than the target, the representation of the target will be only partially activated, and additional neurons will have to be activated to name the target, increasing response time.

### 3.3. Neuroimaging evidence in humans

Neural evidence for number-sensitive coding in humans was provided by Santens et al. (2010, Experiment 1). Participants were presented with dot displays containing one to five dots, and neural activity was measured for each numerosity separately with event-related fMRI. Number-sensitive areas were localized as areas showing increasing activation with increasing number. In order to be sure that we actually detected number-sensitive areas rather than areas that are sensitive to physical parameters that correlate with numerosity (such as total luminance or object size), stimuli were constructed such that confounds of these non-numerical parameters were eliminated. The results revealed a network of bilateral occipital and parietal areas and an area in the medial frontal gyrus. Given that Roitman et al. (2007) found number-sensitive coding neurons in monkey area LIP, we assessed the correspondence of non-symbolic number processing in the monkey and the human brain. We therefore identified areas that functionally correspond to monkey LIP, as assessed with a saccade localizer task. In the area obtained by this localizer task (bilateral posterior superior parietal cortex), number-sensitivity was observed.

## 4. Networks for number representation

Having established the existence of number-sensitive and number-selective in the human brain, we investigated how these different stages are located relative to one another in the human brain, and how non-symbolic and symbolic number representations are related.

### 4.1. Stages of non-symbolic number processing

The computational models proposed three different stages for numerosity processing. In the first stage, the spatial locations of the to-be-enumerated elements are stored in an object location map (Goldberg et al. 2002). This information is then transformed into a number-sensitive code in the second stage, which is subsequently transformed into a number-selective code in the third stage. In Santens et al. (2010, Experiment 1), we observed a larger BOLD signal for larger numerosities in the same area. These areas could correspond either to the object location map or to the number-sensitive code, as both stages show increasing activity for increasing number on the population level. Hence, these studies did not allow distinguishing between the first two stages.

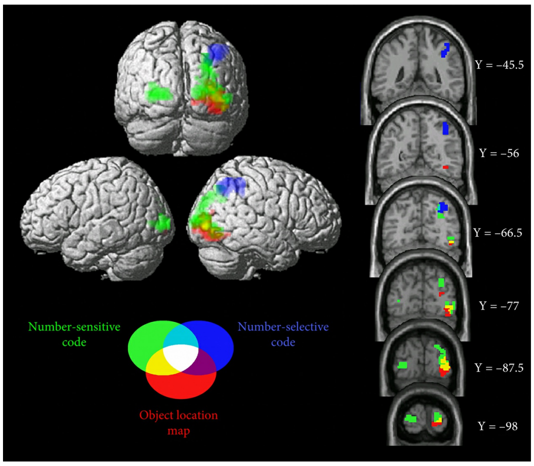

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*Figure 2* : Activation of three different contrasts, each sensitive to one number processing stage: object location map (red), number-sensitive code (green), and number-selective code (blue).

To resolve this issue, we used fMRI adaptation to identify the three postulated stages of numerosity processing and their anatomical location relative to one another (Roggeman et al. 2011). We repeatedly presented the same non-symbolic numerosity (collection of dots) at the same locations in the visual field. In this way, neurons involved in the processing of this numerosity (object location map, number-sensitive, and number-selective neurons) were neurally adapted. Occasionally, a deviant stimulus with a deviant number of dots and/or dots at deviant locations was presented. A factorial design was created in the deviant stimuli, which allowed us to calculate three independent contrasts, each sensitive to one of the three stages. The main result was that the three different stages, tested by three different contrasts, were indeed differently represented in different brain areas along the lines postulated by the model (see Figure 2). The activation of the object location map was present from the earliest parts of the occipito-parietal processing stream. The number-sensitive coding map exhibited a primarily nonlinear pattern of activation, with first increasing and then decreasing activation. The number-selective coding map became more pronounced further along the occipito-parietal processing stream. Such a posterior to anterior gradient along the intraparietal sulcus from number-sensitive to number-selective processing is consistent with the hypothesis that number-sensitive processing is a necessary intermediate processing step for non-symbolic number processing between early visual sensory analysis and a more abstract number-selective system. See Figure 2 for an illustration of the three stages as localized in the human brain.

### 4.2. Pathways for symbolic and non-symbolic number

The model above describes the processing of non-symbolic numbers. The Verguts and Fias (2004) model also concerned symbolic (e.g. Arabic) numbers. To simulate how initially arbitrary symbols can acquire numerical meaning by being associated with non-symbolic numerosities during development, the model was presented simultaneously with non-symbolic numerical input and the corresponding symbols. The latter were directly connected to the number-selective neurons because no nonlinearity is involved in the transformation from symbols to number-selective neurons. After training, it was observed that the number-selective neurons that were tuned to a specific numerosity also responded maximally to the corresponding symbolic input.

However, this representation is accessed through different pathways (Figure 1). For non-symbolic input, visual input is mapped to the object location map, is then followed by number-sensitive coding, and is finally converted in number-selective representations. For symbolic input, in contrast, the mapping from symbol to number-selective code is linearly separable. For this reason, a direct pathway is possible from visual input to number-selective coding, without accessing the object location map and number-sensitive coding system as a necessary preprocessing step. In Santens et al. (2010, Experiment 2), we performed a connectivity analysis on separately acquired fMRI data to test this. We first localized areas that showed an increasing BOLD signal with increasing numerosity, while tightly controlling for different visual parameters. We identified an area in the posterior superior parietal cortex (human LIP) as the neural substrate for the number-sensitive coding system. As the neural substrate for a number-selective representation of number, we selected an area in the IPS which has been localized by both electrophysiological (Nieder and Miller 2004) and neuroimaging studies (Cantlon et al. 2006; Piazza et al. 2004, 2007). Piazza et al. (2007) showed that this representation is shared for symbolic and non-symbolic number (but see Cohen Kadosh et al. 2011; Cohen Kadosh and Walsh 2009). In our whole-brain analysis, we confirmed that this portion of the IPS is indeed activated by numerical stimuli, regardless of the input format. Subsequently, we investigated the functional connectivity of this area using structural equation modeling. It was confirmed that the area in the left IPS to which the number-selective representation of quantity was ascribed (Dehaene et al. 2003), shows a different functional connectivity with visual and number-sensitive areas for symbolic versus nonsymbolic quantities. In particular, the indirect pathway (visual input to number-sensitive to number-selective coding) was stronger for non-symbolic than for symbolic stimuli. In contrast, the direct pathway (visual input to number-selective coding) was stronger for symbolic than for non-symbolic numbers. In Roggeman et al. (2011) and Santens et al. (2010), non-symbolic number activation was bilateral but more pronounced in the right hemisphere. The symbolic stimuli used additionally by Santens et al. mainly activated a left-hemisphere network. This asymmetry may reflect gradients of processing symbolic (left hemisphere) versus non-symbolic (right hemisphere) materials more generally (Gevers et al. 2010; Kosslyn 2006), although this remains to be tested more thoroughly.

Our results revealed an anatomical distinction between number-sensitive and number-selective cortical regions. A number-sensitive processing area was shown in superior parietal cortex. In contrast, the IPS activation that was generated by both symbolic and non-symbolic quantities, was located more anteriorly, at a location that corresponds with activity observed in experiments that specifically investigated number-selective coding (Piazza et al. 2004, 2007). An analogous distinction between number-sensitive and number-selective processing has also been found in electrophysiological experiments in monkeys. Whereas number-sensitive neurons have been found in area LIP (Roitman et al. 2007), number-selective neurons are traditionally found more anteriorly in the IPS (Nieder and Miller 2004).

## 5. Beyond small-number representation: Working memory, task demands, and multi-digit numbers

### 5.1. The object location map as a visual short-term memory system

The model of Verguts and Fias (2004) takes an object location map as input. This is very similar to the concept of a saliency map known from the visual short-term memory literature. A saliency map is a two-dimensional topographic map in which neural activity represents the salient objects in the environment (e.g. de Brecht and Saiki 2006; Ipata et al. 2006; Itti and Koch 2000). The biological reality of such saliency maps has been shown by a number of studies. Bisley and Goldberg (2003) observed that monkey LIP represents attended locations in the visual field. In humans, Connolly et al. (2002) showed that a salience map in the human homologue of monkey area LIP (human LIP) holds a representation of the location of targets, similar to the monkey findings.

A salience map is typically modeled as consisting of a collection of nodes, with each node corresponding to a neuronal population coding for a given location in space. In working memory models, this map is equipped with an active maintenance mechanism implemented as recurrent self-excitation of the nodes (e.g. Grossberg 1980; Usher and Cohen 1999; Wong and Wang 2006). In addition, lateral inhibition between the nodes is implemented to reduce noise in randomly activated nodes. This leads to competitive interactions between the nodes in the map. With an appropriate balance between recurrent excitation and lateral inhibition, a stable encoding of spatial structure of the visual display can be created.

The combination of recurrent excitation and lateral inhibition leads to a maximal set size where all elements are retained. Beyond this set size, information in the map gets lost because of mutual competition. We can think of this maximum set size as the capacity limit of the map. Empirically, such a capacity limit has been observed both in fMRI (Todd and Marois 2004) and in EEG (Vogel and Machizawa 2004; Vogel et al. 2005) signatures. Moreover, different settings of the lateral inhibition parameter lead to different set sizes where the capacity limit is reached. Furthermore, the inhibition parameter functionally defines a threshold for neurons to become activated by input. If the threshold (inhibition parameter) is too low, neurons can be activated by random noise. If the inhibition parameter is too high, genuinely active neurons will be inhibited. Hence, a high level of lateral inhibition leads to precise representations (no noise), but also to a small capacity of the map. Lower levels of lateral inhibition lead to coarser representations (nodes activated by noise), but more items can be stored.

It is known that top down attention is able to bias competitive interactions in visual areas and beyond (e.g. Deco and Rolls 2005; Kastner et al. 1998). A method of controlling lateral inhibition by neurons upstream was recently described in stimulus-sensitive areas, and was suggested to be a principal method also in higher cortical areas (Arevian et al. 2008). Similarly, Edin et al. (2007) proposed that the amount of nonspecific input from upstream to downstream areas can determine working memory capacity.

Putting these pieces together, Roggeman et al. (2010) proposed that the task, and more exactly the representational precision required by the task, can top-down modulate the level of lateral inhibition in the object location / saliency map. The influence of task demands on the activation in a salience map was investigated as a function of set size. For this purpose, the working memory model of Usher and Cohen (1999) was implemented with different settings (high, medium, and low) of the lateral inhibition parameter. The model predictions were then compared with the BOLD activation in human LIP, where the saliency map is housed, in a series of fMRI experiments in which the attention to the items was manipulated. The activation in human LIP in a task that required high, medium or low attention, respectively, to the individual items, was found to be in perfect agreement with the predicted activation of the model with a high, medium or low inhibition parameter.

### 5.2. Symbolic number and working memory

In the previous section, we discussed the object location map / saliency map for locating objects in space and as the basis for spatial working memory. We have shown the mutual dependency between non-symbolic number and the spatial saliency map. In the literature, also the link between symbolic number and space has been discussed extensively. A very robust link between number and space is found in the SNARC effect (Dehaene et al. 1993). In these experiments, it is found that small numbers are responded to faster with the left hand and large numbers with the right hand. Given that numbers are often represented in a left-to-right manner in Western cultures, this observation suggests that numbers are represented spatially, with the small numbers on the left side of space, and the large numbers on the right side of space. Zorzi et al. (2002) demonstrated that patients exhibiting left-side neglect, who neglect the left side of space, also overestimate the midpoints of numerical intervals (e.g. stating that the midpoint between 1 and 9 is 7). In the left-to-right representation of numbers, this observation suggests a corresponding neglect of the small (left) numbers. In addition, many other findings point toward an intimate relation between number and space (e.g., Dehaene et al. 1993; Fischer et al. 2003).

However, in recent years controversy has arisen, demonstrating that identification of number with space representations does not faithfully represent the rich empirical reality. Doricchi et al. (2005) demonstrated that a double dissociation can occur between bisection tasks in physical space and in ‘numerical space’ (cf. van Dijck et al. 2011, 2012; for review see Van Dijck et al. this volume). Recently, Chen and Verguts (2010) proposed that in order to reconcile these findings, it is necessary to assume that a link exists between symbolic number and space, but without assuming an identity relation. This particular model was built on the earlier Gevers et al. (2006) model, but added spatial representations, to which symbolic number representations were connected. Because of the association between number and space, right parietal damage led to number neglect in the model (as in Zorzi et al. 2002). However, because there was merely an association, not an identity relation, between numbers and space, dissociations between the two types of neglect were obtained in the model (as in Doricchi et al. 2005).

The nature of the associations between the spatial system and numbers remains relatively unspecified. One possibility is that it is exactly the same system that is also used for representing object locations, and is used as input for non-symbolic number representation (Section 5.1). Another possibility is that serial position in working memory is spatially coded and that it is this spatial code that is linked to number. This hypothesis is built on the observation that the SNARC effect did not depend on a number’s magnitude but rather on the position of that number in working memory (van Dijck et al. 2011). Moreover, SNARC-like position-space associations can be established for non-numerical stimuli as well as for numbers, with the size of the numerical and non-numerical effects correlating (van Dijck et al. 2011). Further exploration of the validity of these and maybe other possibilities will need computational and imaging efforts in the future.

### 5.3. Adding task demands

Until now, we have only discussed how numbers are represented, and how these representations may be coupled to non-numerical representations. However, behavioral and neural signatures of number processing are almost always measured while subjects are engaged in a task. It is very well possible that also task-specific components leave their signature on the behavioral and neural data. This has been argued extensively in the developmental literature by Thelen, Smith, Schöner and others (e.g. Thelen et al. 2001). In particular, these authors have shown that claims about infant representational capacities must be treated with great caution, because infant performance is very heavily dependent on task demands.

By computationally modeling the different tasks used in the numerical cognition literature, we have come to the similar conclusion that behavioral and neural effects do not immediately inform us about underlying cognitive systems (e.g. Van Opstal and Verguts 2011; Verguts et al. 2005). For example, we have argued (Verguts et al. 2005) that there are different types of distance effects, depending on how the distance effect is measured. The priming distance effect was shown (see above) to emerge from overlap in number-selective representations (see Nieder et al. 2002, and Nieder, this volume, for direct evidence on the existence of such overlap). In contrast, the classic comparison distance effect (i.e. measured as a function of the distance between the relevant numbers in a comparison task; Moyer and Landauer 1967) was shown not to emerge from overlap in representations, but rather from the comparison process (at the decision or response levels). Although this is a rather isolated position in the numerical cognition literature, it connects numerical cognition to related domains, in which theories and models typically ascribe the distance effect as emerging from decision or response processes (e.g. for ordered sequences; Couvillon and Bitterman 1992; Frank et al. 2003; Leth-Steensen and Marley 2000). One prediction is that these two distance effects should in principle be dissociable. We tested this (Van Opstal et al. 2008) by comparing the distance effect in number comparison with the distance effect in letter comparison (for a similar view, see Cohen Kadosh et al. 2008). The classic distance effect was, as predicted, virtually indistinguishable across the two domains; this was predicted because a decision/response process is needed in both. In contrast, the priming distance effect appeared only for numbers, but not for letters.

At an applied level, this theoretical distinction may be important because the comparison distance effect is used increasingly often as a signature of elementary number processing, and correlated with more complex mathematical abilities (e.g. Halberda et al. 2008; Holloway and Ansari 2009; for review see Gebuis and Reynvoet, this volume). Despite the importance of this endeavor, many of the findings currently seem contradictory (but see Noël and Rousselle 2011). In our opinion, a research program looking at individual differences starting from a computationally motivated basis, may shed light on the current controversies. This research program currently remains to be carried out (but see Defever et al. 2011; Sasanguie et al. 2011).

### 5.4. Multi-digit numbers

Finally, a less-studied area of research, especially in computational terms, concerns how multi-digit numbers are represented. Verguts et al. (2005) argued that, because of the very low frequencies of multi-digit numbers, they could not have an explicit representation like small (high-frequency) numbers do. In this view, multi-digit numbers would be represented solely by their single-digit components (for a review see Nuerk et al. this volume); for example, the number 26 would be represented by its digit component 2 and its unit component 6. Moeller et al. (2011) implemented a neural network based on this concept and found that it could account for behavioral data on multi-digit numbers, better than models with a 'holistic' component where multi- (in this case, two-) digit numbers were represented as wholes. A related decomposed-multi-digit architecture was proposed by Grossberg and Repin (2003).

## 6. Concluding remarks

The seminal article of Moyer and Landauer (1967) already ascribed both the distance and size effect for symbolic numbers to a semantic analogue magnitude system. Ever since this article, the concept of an analogue magnitude system for number has been extremely influential in the numerical cognition literature (e.g. Dehaene et al. 1993), up to the current day (e.g. Halberda et al. 2008). Although the concept certainly has its merits, it is our opinion that theories integrating psychology, neuroscience, and computational modeling, are now becoming indispensable. More detailed models need to be developed of how number is represented and processed in the brain. As a first step toward this ambitious goal, we have developed computational models of number processing with ensuing tests of the model predictions. The current chapter reviewed some of this work. In the introduction (Section 1), we described the number-selective coding system, which is the currently most accepted view of number representation. We described psychological and neural evidence for this representation. In Section 2, we discussed our models of core number representation. We showed that the number-selective coding system cannot exist in separation, and that a number-sensitive system is a necessary precursor step in the pathway leading up to a number-selective representation. In Section 3, we described empirical evidence for the existence of a number-sensitive system. In Section 4, we proposed how the different components may relate to one another in brain networks, and we illustrated the connection between the number-sensitive and the number-selective system, both in symbolic and non-symbolic number processing. Finally, we discussed a broader connection to other cognitive structures and processes, including working memory, response structures and multi-digit numbers (Section 5).

Despite our and other people's efforts, the end goal is far from reached. Besides connecting to biology, models need also to connect to complex numerical competencies, such as counting and understanding the natural number system (Ganor-Stern 2012; Widjaja et al. 2011). Such steps have recently been taken from a normative Bayesian point of view (Lee and Sarnecka 2009; Piantadosi et al. 2012). Eventually, the model should be able to explain how humans can work with concepts of number and its derivations, such as infinity, interest rates, and integral calculus (Rips et al. 2008). Moreover, models need to incorporate how number processing relates to other cognitive domains, such as working memory (Piazza et al. 2011), attention and language. Finally, models need to be defined and tested that describe the development of the number domain in children (Feigenson et al. 2002; Piantadosi et al. 2012; Spelke 2000).

Perhaps most importantly, such models should help finding out how number processing is impaired in dyscalculia (Piazza et al. 2010) and related afflictions. By way of comparison, computational models of the basal ganglia and their impairment in Parkinson's disease have helped understanding aspects of the disease and its remediation (Frank 2005; Frank et al. 2004). Ultimately, our goal should be to develop diagnostic tests to probe people and children for a failure in the system in very early stages, before it leads to observable defects. Early and directed intervention can then be developed for these people, in an attempt to remedy problems before they even arise.

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