A Neural Model of How The Brain Represents and Compares Numbers

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A Neural Model of How the Brain Represents and Compares Numbers

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Running Title: Brain representation of numbers

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Abstract

Many psychophysical experiments have shown that the representation of numbers and numerical quantities in humans and animals is related to number magnitude. A neural network model is proposed to quantitatively simulate error rates in quantification and numerical comparison tasks, and reaction times for number priming and numerical assessment and comparison tasks. Transient responses to inputs are integrated before they activate an ordered spatial map that selectively responds to the number of events in a sequence. The dynamics of numerical comparison are encoded in activity pattern changes within this spatial map. Such changes cause a “directional comparison wave” whose properties mimic data about numerical comparison. These model mechanisms are variants of neural mechanisms that have elsewhere been used to explain data about motion perception, attention shifts, and target tracking. Thus, the present model suggests how numerical representations may have emerged as specializations of more primitive mechanisms in the cortical Where processing stream.
Introduction: Human and Animal Numerical Abilities

The roots of modern number system can be traced to the ancient Egyptians and Chinese. The final design of the base-10 system is believed to have been developed by the Hindu-Arabic mathematicians in the 8th - 11th centuries AD. Can one say that this was the beginning of the formation of number sense on earth? In fact, animals managed to survive in challenging environments for millions of years. Choosing a larger prey to hunt, a tree with more fruit, or a flower with more honey required some abilities to estimate and compare magnitudes and quantities in order to choose the one that would enhance survival.

Obviously, people are much more numerically competent than animals, but they have a serious advantage: the symbolic notation. If unable to use either verbal or Arabic notation, humans may perform no better than animals in certain estimation and comparison tasks. Error rates and reaction times in animal data depend on stimulus properties in a manner similar to human data (Dehaene, 1998; Gallistel, 1989). In particular, the Number Size Effect indicates that processing is more difficult for larger quantities or numbers, as reflected in larger reaction times (Figure 1) and error rates. The Numerical Distance Effect shows that comparison among stimuli that differ from each other more in magnitude or quantity results in faster reaction times and fewer errors (Figure 2).

These similarities of animal and human data suggest that common mechanisms control shared numerical abilities. They also raise the question of how numerical estimation abilities may engage more basic neural mechanisms. The present model proposes answers for both types of questions. These results have been presented in preliminary form in Repin and Grossberg (1999a, 1999b).

Several modeling approaches have targeted either exclusively human (McCloskey, 1992; Campbell and Clark 1992; Ashcraft, 1987) or animal data (Meck and Church, 1983). Other models have treated both human and animal data in a more unified fashion (Gallistel and Gelman, 1992). Numerical abilities of human infants have been modeled as well (Wynn, 1998). All of the work above introduced either functional
architectures that allowed a qualitative account for some of data, or simple mathematical formalisms to describe performance as a function of stimuli properties. Dehaene and Changeux (1993) developed the only neural model of elementary numerical abilities. It was based on a previously developed functional model (Dehaene, 1992) and gave a quantitative fit to error rate data from human and animal studies. These models are further discussed and compared with the present model in the next section.

Our Spatial Number Network, or SpaN, model suggests detailed neural mechanisms of numerical mental representations and the dynamic events underlying the processes of numerical information assessment and comparison. Spatial organization and neural mechanisms of the SpaN model can also be compared with neural data about specific brain regions. Using this organization, the model explains both error and temporal characteristics of human and animal experimental data, such as the Number Size and the Numerical Distance effects. It also accounts for number priming data. None of the previous models known to us has quantitatively explained such an extensive empirical data set.

Section 2 gives the overview of relevant data, describes previous modeling and puts the proposed model into the context of contemporary research in the field. Section 3 derives the SpaN model in three steps. Section 4 provides simulations of experimental data. Section 5 discusses the implications of the current work in a broad framework of modeling numerical abilities. Section 6 concludes the article. Model equations are provided in the Appendix.

Experimental data and modeling approaches

Ample evidence is available on the numerical competence of various animal species (for reviews see Dehaene, 1997; Gallistel and Gelman, 1992). For example, animals as simple as honeybees were able to discriminate the amount and frequency of reward in appetitive conditioning experiments (Buchanan and Bitterman, 1988). Pigeons could abstract the information about the relative number of items in small visual arrays, independent of other parameters of the stimuli (Emmerton, Lohmann, and Niemann, 1997). Modality transfer experiments demonstrated that rats could learn the number of events in a visual or auditory sequence (flashes and beeps) and then respond to a mixed auditory-visual sequence with the same total number of events (Church and Meek, 1984). In these studies, numerosity discrimination ability usually dropped with the increasing number of items, thereby showing the Number Size effect.

Primates were even able to perform simple arithmetic: In the experiments by Washburn and Rumbaugh (1991), chimpanzees could choose the pair of two piles of chocolate bits that had a bigger total number of bits, even though each individual pile in the chosen pair had fewer pieces than the largest pile in the second pair. More mistakes were made with decreasing difference in the number of bits, thereby showing the Numerical Distance effect.

Animal studies provided the most valuable data since they were unbiased and bore little influence of higher-order cognitive interference. However animal data provide little or no chronometric information for numerically related tasks. Reaction time data were obtained mostly in the psychophysical experiments with human subjects. Number reading studies (Bryzbaert, 1995) and subitizing (rapid numerosity estimation of the visual array with a small number of items, usually up to three or four) experiments (Mandler and Shebo, 1982) reported an increase in reaction times for bigger numbers and larger arrays, thereby demonstrating the temporal side of the Number size effect. Many
studies addressed single-digit (Parkman, 1971), two-digit (Dehaene, Dupoux, and Mehler, 1990; Link, 1990; Bryzbaert, 1995), and multi-digit (Poltrock and Schwartz, 1984) number comparisons that showed longer reaction times for smaller distances between numbers for most cases, thereby demonstrating the temporal side of Numerical Distance effect. The amount of priming in number priming experiments was also shown to be a decreasing function of the numerical distance from the prime to the target number (den Heyer and Briand, 1986).

Data from brain-lesion patients provided many important insights about the structural composition of numerical abilities, such as the dissociation of verbal and quantitative knowledge, or of subitizing and counting (Dehaene and Cohen, 1994; 1997). Together with the psychophysical data from human infants and adults, and various animal species, they have provided explanatory targets for models of human and animal numerical abilities. Table 1 summarizes the most influential and widely cited models. The classification is based on the domain of application (function, mechanism and representation addressed) and the experimental data explained. The table also includes the new SpaN model.

Models by McCloskey and colleagues (McCloskey, 1992, McCloskey and Macaruso, 1994), Ashcraft (1987, 1992), the encoding complex hypothesis by Campbell and Clark (1992; Clark and Campbell, 1991), and the triple-code model of Dehaene (1992) may be referred as functional models. They considered high-level verbal, phonological, graphemic representations and complicated cognitive tasks, including numerical calculations. A wide variety of human data were explained qualitatively.

The model of Gallistel and Gelman (1992), which was based mostly on animal data, attempted to link principles of animal cognition to adult numerical competence. They considered the implications for development of numerical abilities and qualitatively accounted for such phenomena as subitizing, judging the order of two digits, and retrieving number facts. Their model used the mechanism of preverbal counting proposed by Meek and Church (1983) for duration and numerosity estimation in rats that had explained the cross-modal transfer findings. Wynn (1998) used a similar mechanism in her model of infant numerical abilities.

The Meek and Church (1983) information-processing model of counting and timing relied on a serial mechanism of numerical information accumulation. In the model, a pacemaker generates equally spaced pulses. Before reaching the accumulator, these pulses are gated by a mode switch, which operates either in a run or a stop mode for duration estimation, or an event mode for counting. The basic idea is that the switch lets through a certain number of the pulses that are endogenously generated by the pacemaker through time. The accumulator adds up the pulses that are let through. The accumulator activation is read out to working memory, where it is compared to a reference memory and incorporated into the decision process.

![Functional organization of the model by Meek and Church (1983).](image)
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Table 1. Key models of numerical cognition.
The neural network model proposed by Dehaene and Changeux (1993) addresses the development of numerical competence in humans and animals. It suggests a detailed approach for numerosity extraction from the visual input stream. Objects in the scene are coded as Gaussian distributions, which then are projected onto a two-dimensional array of Difference-of-Gaussian (DOG) filters representing the retina. The cumulative activation of this array over all spatial locations activates the numerosity detectors that are implemented as nodes with increasing thresholds. Different threshold levels roughly correspond to different numerosities. Parallel processing by means of a retina-like mechanism was mainly supported by the evidence from subitizing (e.g., Mandler and Shebo, 1982). Auditory input activation is assumed to come from “echoic” memory and to add up with the visual stream activation represented by the DOG array cumulative signal. Simulations provided quantitative results that could be compared to response distribution data from animal and human studies. Additional output clusters allowed training the network with pairs of numerosities to simulate number comparison. When a set of numerosities has been presented, the connection strength from numerosity detectors to output clusters is altered through learning to predict the error rates for comparison process.

The SpaN model embodies a neural network architecture for modeling the representation of numerical information in the brain. There are three key features that put the model into its own niche in the field. First, it describes the dynamics of the mechanisms of number acquisition and comparison on the scale of milliseconds; thus it explicates the numerical process microstructure, as opposed to learning, which reflects its macrostructure. Second, the SpaN model simultaneously provides a quantitative fit to error rate and reaction time data, what has not been done before with a single computational model. Finally, the neural mechanisms used in the model are specialized combinations of mechanisms that have previously been used to model processes of spatial representation and motion perception (Chey, Grossberg, and Mingolla, 1997, 1998; Grossberg and Kuperstein, 1986/1989; Grossberg et al., 1997). The model hereby clarifies how numerical abilities may have arisen from more general processes in the Where or How stream of the brain (Goodale and Milner, 1992; Mishkin, Ungerleider, and Macko, 1983).

**Three easy steps to SpaN model**

The SpaN model has three main processing stages: preprocessor, Spatial Number Map, and Comparison Wave. A block-diagram of the processing steps is shown in Figure 5. The preprocessor transforms sensory information through visual, auditory or tactile streams into an amplitude code by using a combination of input transient detectors and integrators (or accumulators). The Spatial Number Map converts the amplitude code into a spatially ordered representation of number. Temporally changing patterns of activation...
across the Spatial Number Map represent information related to numerical judgments. The Comparison Wave uses these temporal changes in Spatial Number Map activation to make numerical comparisons exhibiting properties that explain error rates and reaction time data. The following sections describe model details.

Figure 5. Functional diagram of the SpaN model.

Stage 1: Preprocessor

The preprocessor converts sensory input in different modalities into an analog signal, whose amplitude represents the number of items in a spatial pattern or the number of events in a temporal sequence. Each item in a spatial pattern or event in a temporal sequence generates an input. Increments of this input are converted into transient outputs.
In this way, a continuously changing input can be transformed into a discrete series of output bursts. These output bursts are then added by an integrator, or accumulator, neuron, or population of neurons. The amplitude of accumulator activity represents the total number of transient bursts (Figure 6).

This mechanism plays a functional role similar to the spatial filtering used in Dehaene and Changeux (1993) and the gated pacemaker with accumulator proposed in Meck and Church (1983). Transient cell responses are a common feature at the front end of models aimed at explaining data about visual motion perception, spatial attention shifts, and target tracking (Baloch and Grossberg, 1997; Baloch et al., 1999; Chey, Grossberg, and Mingolla, 1997, 1998; Grossberg, 1998). This mechanism is realized in a simple way in the SpaN model (see Appendix for equations) to portray an early stage of input preprocessing. Visual, auditory, or tactile sensory streams may produce different analog signals that are physically generated in different brain areas. The key issue is that the amplitudes of these signals are related to numerical properties of the stimuli in each modality. It is assumed in the model that the same numerosities in different modalities produce similar outputs after the integration of transients.

Stage 2: Spatial Number Map

Many experimental studies have provided evidence for the idea that there exists an inherently approximate analog representation of numerosities in the brain (see Dehaene, 1997 for an overview). The hypothesis that this representation is modality-independent on the lowest cognitive level is supported by modality transfer experiments with rats (Church and Meck, 1984) and pigeons (Emmerton, Lohmann, and Niemann, 1997). In these studies, animals were able to extract the numerical properties from the stimuli in visual and auditory modalities, and then to combine the numerical information on an abstract level to produce the response. Human adults can abstract numbers with little effort. Even 6-8 month old infants are able to select visual displays that match numerically identical auditory patterns (Starkey, Spelke, and Gelman, 1983).

The concept of an amodal representation being distributed over several spatial locations appeared in the model by Dehaene and Changeux (1993). Recent brain imaging data (Dehaene et al., 1996; Pinel et al., 1999) confirmed the inferior parietal cortex (IPC) as a convergence zone during various numerical tasks with inputs and outputs representing different modalities. IPC and adjacent regions are known to play an
important role in various spatial tasks: visuomotor integration (Nishitani et al., 1999),
navigation (Frith and O'Keefe, 1998), location working memory (Cournetey et al., 1996),
and tactile object recognition (Deibert et al., 1999). Spatial attentional deficits are also
believed to be associated with IPC damage (Buck et al., 1997). All this evidence
strengthens the spatial hypothesis for the amodal numerosity representation. In parietal
cortex, spatial relations are often exhibited in the form of spatial maps (Andersen, Essick,
and Siegel, 1985). The use of transient cells to preprocess inputs to the Spatial Number
Map is consistent with the fact that such preprocessing of visual motion, attention, and
tracking is part of the Where cortical stream to which IPC belongs.

Numerical organization in humans is known to have ordering and directional
properties. The experiments by Dehaene and colleagues (Dehaene, Bossini, and Giraux,
1990; Dehaene, Dupoux, and Mehler, 1993) demonstrated that left-hand side responses
were faster than right-hand side for the smaller numbers within a given set of numbers,
and conversely for the larger numbers. This effect, called SNARC (Spatial-Numeric
Association of Response Codes), implies that left-to-right representation exists for
numbers going from small to large, at least for subjects raised in Western cultures, while
for middle eastern subjects (e.g., Iranians) the effect was less pronounced or reversed. A
similar directional dependence was reported by Bryzbaert (1995), who found that
subjects were faster to respond to the left-to-right ordered pairs (24 26) than to the pairs
ordered inversely (26 24).

Taking into account the above evidence, it is reasonable to assume that a Spatial
Number Map is the basis for analog representation of numerical information. In the SpaN
model, the Spatial Number Map is implemented as a linear array of cells, where every
cell receives its input through a nonlinear signal function before activating excitatory
and inhibitory on-center off-surround kernels (Figure 7). Both the thresholds and the slopes
of the transfer functions increase from left to the right side of the map (cf. Grossberg and
Kuperstein, 1986/89). Each cell receives the same analog input from the integrator
neurons of the preprocessor. As the input stays on, a certain pattern of activation builds
up across the map cells (see Appendix for equations). Patterns of activation are sharper
and at leftward positions for smaller inputs, and broader and at rightward positions for
larger ones; the model hereby complies with Weber's law, which says that the variance
covaries with the mean position. The asymmetry in the output activations is similar to
what is observed in the empirical data (see Simulation Results section for details).

Stage 3: Comparison Wave

Presentation of the next stimuli, when activation of the previous one has not yet
decayed completely, is a common practice in numerical comparison experiments. Within
the Spatial Number Map, this causes a dynamical redistribution of the activation patterns
across the map. For example, suppose that a small number is presented first and produces
activation on the left side of the map (Figure 8). A larger number presented next would
build its activation at some location to the right of the smaller one, while some signal
remaining from the small number is still decaying. The net effect of this correlated, but spatially displaced, growth and decay of activation is a bell-shaped activation that moves continuously from one spatial location to the other. We call this a traveling wave of activation a Comparison Wave and suggest that this dynamical redistribution of activation underlies the process of numerical comparison. Similar traveling waves have been used to explain many data about motion perception, spatial attention shifts, and target tracking (Baloch and Grossberg, 1997; Francis and Grossberg, 1996; Grossberg 1999; Grossberg and Rudd, 1989, 1992). Link (1992) used a random walk process to generate comparisons between stimuli. Such a random walk has some properties of a Comparison Wave.

In the comparison waves of the SpaN model, a larger numerical distance between the stimuli implies a more distant separation of their representations within the map. Consequently, a bigger comparison wave is generated. Most of the brain-imaging techniques (PET, fMRI) do not yet possess a sufficient temporal resolution (on the order of 10-100 ms) to support or disprove this view. Several ERP studies (Ullsperger and Grune, 1995) have, however, detected smaller P300 amplitudes for smaller numerical distances.

To selectively detect the direction of the Comparison Wave, another population of cells receives input from the Spatial Number Map. Each cell in this population is sensitive to either the right or the left direction of motion of activation across the Spatial Number Map. Then the activations of all right direction-sensitive cells are added up to yield the right Comparison Wave output, while outputs from all left direction-sensitive cells add to yield the left Comparison Wave output. If the Comparison Wave to the left is larger, then “smaller” is the judgment; if the right wave wins, then “larger” is the judgment (Figure 9). Greater distances between the patterns in the Spatial Number Map give rise to bigger Comparison Waves, which conforms to the

![Figure 8. Computer simulation of the dynamic redistribution of activation across the Spatial Number Map through time. Different line styles correspond to different times (in the integration step units).](image)

![Figure 9. Computer simulation of the Comparison Wave. Second input is smaller than the first one, so the wave moving to the left wins (dashed line). The response is related to the striped area under the curve (see Appendix for details).](image)
experimental findings about P300 that were mentioned earlier. The details of how these mechanisms can quantitatively explain psychophysical data are discussed in the next section.

**Simulation Results**

The simulations were implemented in MATLAB environment and run on a 300MHz PentiumII PC. An array of 120 nodes was used for both the Spatial Number Map and the Comparison Wave direction-sensitive cells. Throughout the simulations, all free parameters in Equations 1-11 of the Appendix were fixed (see Appendix for parameter values). Thresholds and slopes of the Spatial Number Map were chosen to obtain the best fit for data in Figure 10. All target data are plotted as dashed lines, all model results as solid lines.

**Error rate data**

The most informative experimental studies provide not only error rate data, but also the complete response distribution. In the work of Mechner (1958), rats were trained to press a lever for a fixed number of times in order to get a reward. Data points (Figure 10) represent the proportion of responses made to match one of the four required fixed numbers of lever presses of 4, 8, 12, or 16 (dotted lines).

The basis of numerical information representation in the model is the Spatial Number Map. Its patterns of activation reflect the differences of processing of different numerical judgments. When the stimulus is present for a sufficient amount of time, and the required response has to be produced without any time constraints, the model assumes the response distribution to be directly related to the equilibrium activation pattern of the map. Figure 10 (solid lines) shows the map activation for the four stimulus magnitudes related as 4:8:12:16. The patterns for bigger numerosities are more distributed along the map, as in the data. There is also a small bias towards larger stimuli, which is reflected in the asymmetry of the distributions: they have more activation to the right of the mean than to the left.

The Numerical Distance effect exhibits itself through experiments wherein two stimuli with different numerical properties are used in each trial. The response error rate is evaluated as function of the numerical distance between numbers or quantities of objects, which is varied throughout the experiment. The studies demonstrate that the error rate is higher for adjacent numbers and then goes down for the numbers further apart.
Figure 11A shows the data for humans comparing two-digit numbers and chimpanzees selecting the larger of two piles of chocolate bits.

In the SpaN model, presentation of two inputs in a single trial generates a Comparison Wave as a result of the transition between the successively activated input representations within the Spatial Number Map. Both left and right waves may appear during the process of redistribution of activation across the map, but the wave with larger magnitude wins and thereby provides the information about the direction of the comparison process. The model suggests that the response time in comparison tasks depends on the rate with which the Comparison Wave builds up. This rate can vary both as a function of stimuli magnitude and the difference between consecutive stimuli. The motor part of the response (e.g., the key press) is assumed to be equal for all numerical stimuli.

The first input (equal to 6 units) is presented to the network for a fixed time (450 time steps). After a brief delay (100 time steps) the second input is presented. Accumulation of the signals from directional-sensitive cells starts at the same time (see Equations 10 and 11 in the Appendix). The accumulation process lasts for a fixed number of time steps (T = 200) for each input, and the maximum magnitude \( g_{j}^{\text{max}} = \max\{g_{j}^{\text{right}}, g_{j}^{\text{left}}\} \) of the two waves is recorded. The larger the amplitude of the Comparison Wave in one direction with respect to the other direction, the more reliable and accurate is the response. Figure 11B shows the plot of the inverse of the \( g_{j}^{\text{max}} \) for different pairs of inputs, where “6” was always presented first followed by one of the inputs 2, 3, 4, 5, 7, 8, 9, or 10. The smallest Comparison Waves (largest inverse values of \( g_{j}^{\text{max}} \)) occurred for the inputs closest to “6,” with the fall-off slowing down with increasing distance from “6.” The results of these simulations exhibit similar properties to those found in the experimental data (see Figure 11A).

Chronometric data

The SpaN model is a real-time model that incorporate time as an explicit independent variable. Thus it can simulate the microstructure of the processes underlying numerical abilities including data about reaction times. For data matching purposes the
Spatial Number Map output (in integration time step units) is always scaled uniformly by
the factor of ½. It is then shifted by a fixed amount \( t_{\text{const}} \) to account for the processes
assumed equal for all the input stimuli, which can be the time needed for a motor
response or for visual processing of a one-digit number.

In many experimental paradigms, number-reading times can be assessed with the
help of an eye-tracking technique. The duration of fixation on the numerical stimuli gives
the time needed for cognitive processing minus the visual system processing time. The
latter can be assumed as being equal for single-digit numbers in Arabic form. Figure 1
diamonds, dashed line – best linear fit) displays the first-gaze duration (FGD) times in
Arabic number reading experiments. Here, the Number Size effect yields an
approximately linear increase in reading time with number magnitude.

The SpaN model assumes that number reading times are related to the rate of
activity build-up in the Spatial Number Map, which is implemented according to
Equation 6 in the Appendix. When the map activation reaches a threshold, which is fixed
for all inputs, the number of elapsed time steps \( t_{\text{model}} \) is recorded and then transformed
before plotting it on the Y-axis as \( t_{\text{plot}} = t_{\text{const}} + \frac{1}{2} t_{\text{model}} \). Figure 1 shows simulation results
for inputs with the magnitude ranging from 1 to 10 (circles, solid line – best linear fit). The
results are comparable to experimental data and exhibit a similar linear increase in reaction time with increasing stimulus magnitude.

Experiments wherein the two stimuli are presented with a short delay between
them, allow estimation of priming effects. For such stimuli as numbers, two types of
priming are known. The first one is semantic priming, where the response time for
number-number pairs is contrasted with that of number-letter pairs. The second type of
priming is observed for number-number pairs, when the numerical distance between the
numbers in each pair is varied. The second type of priming reflects the temporal side of
the Numerical Distance effect and has been demonstrated experimentally to be a linear
function of a prime-target

Number priming results are obtained from the dynamics
of the Spatial Number Map. The first input (prime) is
selected from the set of inputs of 1 through 15, and is
presented for a fixed time (450 time steps). The second input
(target) is presented after a brief delay (100 time steps).
Reaction time is measured from
the onset of the target input to
the moment when the Spatial
Number Map activation reaches
a fixed threshold. Simulation
results for two target inputs “5”
and “8” are shown in Figure
12B. Priming is a linear

![Figure 12. Number priming. Data (panel A): dashed line is the best linear fit, adapted from Brysbaert (1995). Model (panel B), circles – target “5,” diamonds – target “8”; lines represent best linear fit to five data points.](image-url)
function of the distance from target in a limited region around the prime, then it flattens out for bigger distances.

The Number Size and Numerical Distance effects may also be derived from temporal characteristics of the numerical comparison process. Experimental data suggest that for a fixed distance between the pair of numbers, the comparison time increases as the magnitude of the numbers increase; i.e., to compare “3” and “5” takes less than to compare “6” and “8.” Figure 13 (filled diamonds, dashed line - best linear fit) demonstrates the effect for single-digit number comparisons.

To simulate this effect, two inputs were presented to the SpaN model. The first input was presented for a fixed time (450 time steps), the second one followed with a 100 time step delay. Number pairs in the range from (3,5) to (10,12) with a constant distance of two units between them served as the inputs. Eight input pairs were presented to the network in both ascending (3,5) and descending (5,3) order. Figure 13 gives the times when the Comparison Wave magnitude had reached a fixed threshold for both right and left directions (open circles - right, open diamonds - left; solid lines - best linear fits). The reaction time increase is linear with number magnitude, which is similar to the empirical data.

The influence of the numerical distance on the comparison time was studied in experiments, wherein two-digit numbers in Arabic notation were visually presented to human subjects. Figure 2 (diamonds, dashed lines) shows the longest comparison times for nearby numbers, and a rapid decrease for bigger interstimuli distances. In the SpaN model, presentation of the pairs of inputs (2,6), (3,6), (4,6), (5,6) and (6,7), (6,8), (6,9), (6,10) to the network were used to simulate comparison time dependence on the interstimuli distances. The same temporal characteristics of the stimuli as in the previous simulation were used. Response times were recorded at the moment that the bigger of either the left or the right Comparison Wave reached a fixed threshold. Figure 2 (circles, solid lines) demonstrates that the reaction time drop was faster closer to the common stimuli (input equal to six units) and slowed down further away from it in the same fashion as in the experimental data.

**Discussion**

The SpaN model proposes a neural architecture for modeling basic facts of numerical competence that are shared by human and animals. The model uses specialized versions of mechanisms - such as transient cells, spatial maps, and comparison waves - that have also been used to model many different types of data concerning the Where/How cortical processing streams. Using these mechanisms, key experimental paradigms about numerical estimation and comparison can be simulated, and quantitative estimates for error rates and reaction times can be obtained. The model targeted the
explanation of the extensive set of empirical data. Most of the simulations captured the behavior of a psychophysical variable in the whole range of the stimuli employed (see Simulation Results section). The exception was priming data (Figure 10). Here, only a range of numbers, centered at the stimulus-prime, exhibited the experimentally demonstrated linear increase in reading time, while larger prime-target distances resulted in no or little priming as opposed to the linear priming that is observed (Bryzbaert, 1995). The following hypothesis provides a possible explanation: Cognitive processing of two-digit numbers may depend on the other properties of the stimuli, like the number of digits (indicated in Bryzbaert, 1995). This may imply that the two-digit number is not processed all at once, but a dissociation occurs between processing of each of the two-digits. Thus, the priming effect cannot be fully attributed to number magnitude, because part of the effect may come from a categorical perception of numbers that is due to interactions between the separate processing of each digit. Given the above assumptions, the model results can be interpreted as a genuine magnitude-related priming, which is valid for small numbers, or for a certain range of numbers, that is not influenced by composite categorical-magnitude processing. We are now developing a model of multi-digit number representation using the SpaN model as a basic module.

Another possible subtlety in the data explained is the approximately linear increase in number reading times (Figure 1) that was similar to gaze duration times for single digit reading (Gielcen, Bryzbaert, and Dhont, 1991). Some psychophysical studies reported logarithmic behavior with respect to number magnitude, such as subitizing experiments (Mandler and Shebo, 1982), and one and two-digit number reading experiments (Bryzbaert, 1995). Other properties of the stimuli, rather than their magnitude, could have contributed to the results in some cases. For example, there could be parallel rather than serial visual processing mechanisms operating in the subitizing and digit-number of digits studies.

Overall, the SpaN model explains similar set of error rate data as the model of Dehaene and Changeux (1993). On the other hand, the Comparison Wave mechanism that we propose is a conceptually different approach from the one by Dehaene and Changeux that learning in connection weights occurs between pairs of numerosities. These approaches are not necessarily mutually exclusive, but may be complementary. The Comparison Wave addresses the microstructure of the process on a millisecond time scale, while the learning process targets the developmental issues on a time scale of days or even years.

In addition to error rates, the SpaN model goes beyond the scope of previous models by accounting for four different types of chronometric data. The reaction time information is read out from the different parts of the model: from the Spatial Number Map for reading times and priming, and from the Comparison Wave for numerical comparison tasks. We hypothesize that these two output pathways are used to estimate different sorts of information about numerical estimation and comparison much as the form and motion systems are used to estimate different types of information about individual and sequential visual scenes. Common temporal scale in all simulations is an important feature, since the same transformation of integration time steps into milliseconds is used in each case, thus providing a common linking hypothesis between the two types of data.
Appendix

Preprocessor

The transient cell response is calculated as the product $xz$, where the cell activation increases as a function of input $I$, and the transmitter gate $z$ habituates, or depresses, as a function of $x$ (Baloch et al., 1999; Grossberg, 1972; Ogmen and Gagne, 1990). In particular, the time-averaged activity $x$ is computed by a leaky integrator with a time constant $A$, where the input $I$ takes the form of a rectangular pulse and $\gamma$ is a constant tonic level:

$$\frac{dx}{dt} = -Ax + I + \gamma.$$  \hspace{1cm} (1)

The habituative transmitter gate $z$ accumulates at rate $B$ to a target level $I$, and is inactivated, released, or depressed by the mass action coupling $-C[x]^+z$ with activity $x$:

$$\frac{dz}{dt} = B(1 - z) - C[x]z.$$  \hspace{1cm} (2)

In (2), rates $B$ and $C$ are constant, and $[x]^+ = \max(x, 0)$. The activity $y$, which is the final output of the Preprocessor, integrates (or sums, in the discrete time formulation) the products $xz$ over a threshold value $y_{l=0}$:

$$y = \sum_{l \geq 0} \left[ xz - y_{l=0}^+ \right].$$  \hspace{1cm} (3)

The amplitude of this integrated signal is roughly proportional to the number of items or events in a sequence, so that the output reflects numerical properties of the input. Parameter $T$ in (3) represents the total time while the input is present. The initial conditions for Equations (1) through (3) are $x|_{t=0} = \frac{\gamma}{A}$, $z|_{t=0} = \frac{B}{B + C\gamma/A}$, and $y|_{t=0} = x|_{t=0} \cdot z|_{t=0} = \frac{\gamma}{A} \cdot \frac{B}{B + C\gamma/A}$ in order to eliminate the DC component in the integrator final output.

Spatial Number Map

The Spatial Number Map is implemented as a linear array of nodes, where the input $s_i$ to each node equals:

$$s_i = \frac{\left[ y - \Gamma_i \right]^+}{\alpha_i^+ + \left[ y - \Gamma_i \right]^+}.$$  \hspace{1cm} (4)

In (4), $i$ is the node position along the map ($i=1$ being the leftmost node), $y$ is the integrator output in Equation (3), the $\Gamma_i$ are thresholds that increase from left to right, parameters $\alpha_i$ control the slope increase from left to right, and parameter $n$ determines how steep the slopes are (see Figure 7 for transfer function examples).

Normalization of the inputs $s_i$ preserves their relative sizes while also ensuring the same order of magnitude for values on the left and right sides of the map:

$$S_i = \frac{s_i}{\sum_k s_k}.$$  \hspace{1cm} (5)

In (5), the summation over $k$ spans all the map nodes. The normalized input $S_i$ activates $p_i$ of the Spatial Number Map via an on-center off-surround network:
\[
\frac{dp_i}{dt} = -Dp_i + (1 - p_i) \sum_k F_{ik} S_k - p_i \sum_k G_{ik} S_k. \tag{6}
\]

In (6), \(D\) is a constant decay rate, and \(F_{ik}\) and \(G_{ik}\) define excitatory and inhibitory kernels, respectively. Excitatory and inhibitory sums in (6) are gated by the membrane equation, or shunting, terms \((1 - p_i)\) and \(-p_i\), respectively. Summation over \(k\) spans all nodes where kernels have nonzero values. The initial condition is \(p_i|_{t=0} = 0\), since no spontaneous activity is assumed to be present. The excitatory and inhibitory kernels for different locations on the map obey:

\[
F_{ik} = \frac{F}{\sigma_k \sqrt{2\pi}} \exp\left\{-\frac{1}{2} \left(\frac{k-i}{\sigma_k}\right)^2\right\}, \quad G_{ik} = \frac{G}{\zeta_k \sqrt{2\pi}} \exp\left\{-\frac{1}{2} \left(\frac{k-i}{\zeta_k}\right)^2\right\}. \tag{7}
\]

They are shown in Figure 7. In (7), parameters \(F\) and \(G\) are constant, and \(\sigma_k\) and \(\zeta_k\) increase from the left to the right side of the map. Figure 10 shows the activations \(p_i|_{t=\infty}\) for different values of the integrator output that correspond to increasing numerical magnitude of the input stimulus.

**Comparison Wave**

Two arrays of nodes with activities \(q_i^{\text{right}}\) and \(q_i^{\text{left}}\) transform the outputs \(p_i\) of the Spatial Number Map into left and right Comparison Waves. The direction-sensitive activities \(q_i^{\text{right}}\) and \(q_i^{\text{left}}\) detect the redistribution of activation patterns across the Spatial Number Map through time:

\[
\frac{dq_i^{\text{right}}}{dt} = -E q_i^{\text{right}} + \left[p_{i-m}(t) - p_{i-m}(t-1)\right]^+ \cdot p_i(t) \tag{8}
\]

and

\[
\frac{dq_i^{\text{left}}}{dt} = -E q_i^{\text{left}} + \left[p_{i+m}(t) - p_{i+m}(t-1)\right]^+ \cdot p_i(t). \tag{9}
\]

In (8) and (9), index \(l\) reflects the cell position in the array, \(E\) is the time decay rate, \(m\) is a constant shift value, and \((t)\) and \((t-1)\) denote current time and the time one integration step back. This direction-detection mechanism computes the product of activation \(p_i(t)\) at current node \(l\) and the phasic change of activation \([p_{i+m}(t) - p_{i+m}(t-1)]^+\) (a derivative-like operation) at the node shifted to the \(m\) positions to the left (+) or to the right (-) from the node \(l\). The activities \(q_i^{\text{right}}\) (\(q_i^{\text{left}}\)) are added to compute the right and left outputs \(g_i^{\text{right}}\) (\(g_i^{\text{left}}\)) from the Comparison Wave at any given time, namely:

\[
g_i^{\text{right}} = H \sum_{t=0}^{T_r} \sum_{k=1}^{M} q_k^{\text{right}} \tag{10}
\]

and

\[
g_i^{\text{left}} = H \sum_{t=0}^{T_r} \sum_{k=1}^{M} q_k^{\text{left}}. \tag{11}
\]

This Comparison Wave sums the \(q_i^{\text{right}}\) (\(q_i^{\text{left}}\)) values up to response time \(T_r\). \(H\) is a constant scaling factor, \(M\) is the total number of left or right direction-sensitive nodes, which in turn equals to the number of nodes in the Spatial Number Map.

Parameter values were fixed for all simulations: \(M=120\), \(A=10\), \(B=0.05\), \(C=5\), \(D=0.7\), \(E=2\), \(F=1\), \(G=0.0004\), \(K=800\), \(\gamma=20\), \(n=4\), \(m=10\); for \(k=1,\ldots,120: \sigma_k=32+0.07\cdot k\), \(\zeta_k=3.2+0.07\cdot k\), \(\Gamma_k=0.23+0.17\cdot k\), \(\alpha_k=1.98\cdot 10^4+2.87/(k-282)\).
References


