# Development of Elementary Numerical Abilities: A Neuronal Model

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## Abstract

■ Despite their lack of language, human infants and several animal species possess some elementary abilities for numerical processing. These include the ability to recognize that a given numerosity is being presented visually or auditorily, and, at a later stage of development, the ability to compare two numerosities and to decide which is larger. We propose a model for the development of these abilities in a formal neuronal network. Initially, the model is equipped only with unordered numerosity detectors. It can therefore detect the numerosity of an input set and can be conditioned to react accordingly. In a later stage, the addition of a short-term memory network is shown to be sufficient for number comparison abilities to develop. Our computer simulations account for several phenomena in the numerical domain, including the distance effect and Fechner's law for numbers. They also demonstrate that infants' numerosity detection abilities may be explained without assuming that infants can count. The neurobiological bases of the critical components of the model are discussed. ■

## INTRODUCTION

Arithmetic is a fundamental conceptual achievement of the human brain. Over the last decade, the roots of our concepts of number have been traced experimentally to their precursors in animals and in human infants (for review see Gallistel & Gelman, 1992). In parallel, psychological experiments with adults and brain-lesioned patients have started to reveal the neuropsychological architectures that underlie our ability to process numbers (for reviews see Dehaene, 1992; McCloskey, 1992).

Most human mathematical achievements result from the development and mastery of a complex notation system. Yet a minimal set of principles of elementary arithmetics, shared with several animal species, seems to precede and perhaps guide these higher-level language-based faculties (Dehaene, 1992; Dehaene & Mehler, 1992; Starkey, 1992; Wynn, 1992). As will be described below, many animals are sensitive to numerical regularities in 'heir environments, can represent these regularities internally, and can perform elementary and approximate computations with numerical quantities (reviews in Davis & Pérusse, 1988; Gallistel, 1990). Similar abilities are found in human infants in their first year of life, well before they begin to produce language (e.g., Starkey & Cooper, 1980). Finally, in a severely aphasic and acalculic patient with an extensive lesion in the left hemisphere, Dehaene and Cohen (1991) found a selective preserva-

tion of elementary numerical abilities for representing numerical quantities and for comparing them, while the formal language-based calculation abilities were lost.

These converging lines of evidence suggest the existence, in the animal and human brain, of specialized neural systems for processing numbers on a nonlinguistic basis. The detailed implementation of these neuronal systems, however, remains largely unknown. The aim of the present paper is to describe a simple, yet plausible, model for the implementation of elementary numerical abilities in a formal neuronal network. In this respect we build upon a framework that we have progressively developed over the last years and that has been primarily applied to the modeling of prefrontal cortex functions (Dehaene & Changeux, 1989, 1991). Starting from behavioral and anatomical data, we try to delineate elementary principles of neural architecture that give rise to a defined function. We implement these principles into a minimal formal model that provides a highly simplified view of the relevant biological mechanisms, yet incorporates plausible anatomical, cellular, or molecular components (Changeux & Dehaene, 1988). In addition to offering clues for the understanding of psychological and neurobiological data, the ultimate goal of our approach is to generate precise and testable predictions that might be examined experimentally using electrophysiological or behavioral techniques.

Here we restrict ourselves to modeling the most ele-

mentary of numerical abilities: the approximate recognition of the numerosity of a set of objects and the comparison of two numerosities. We shall also examine the developmental sequence of these abilities in human infants. The paper is organized in six main sections. The first section briefly reviews the relevant experimental data. Then we describe the functional architecture of the model and the main principles on which it is based. Finally we describe detailed simulations of our model in an incremental fashion, starting with the most elementary abilities common to all species and progressively moving to higher abilities that develop in human infants during the first year of life.

## EXPERIMENTAL DATA RELEVANT TO ELEMENTARY NUMBER PROCESSING

In this section, we briefly review the main data (D) on elementary number processing in animals, human infants, and adults, that we consider relevant to our model.

### D1. Infant Numerosity Detection

Four-day-old to 7-month-old human infants can discriminate sets of visual objects of varied shapes and sizes on the basis of their numerosity alone (Antell & Keating, 1983; Davis & Ashmead, 1991; Starkey & Cooper, 1980; Strauss & Curtis, 1981; Treiber & Wilcox, 1984; van Loosbroek & Smitsman, 1990). Discrimination is reliable for numerosities of 1 vs. 2 and 2 vs. 3. It is less often observed with 3 vs. 4 and 4 vs. 5, and it systematically fails for 4 vs. 6. In the auditory modality, 4-day-old infants discriminate bisyllabic from trisyllabic words, even when their durations are equalized (Bijeljac-Babic, Bertoncini, & Mehler, 1991). These data have been taken to suggest that newborn infants are innately equipped with "numerosity detectors" (Cooper, 1984) at least for numerosities up to 3 or 4.

### D2. Cross-Modal Infant Studies

Cross-modal matching experiments suggest that, in 6- to 8-month-old infants, numerosity detection occurs regardless of the input modality. For instance when hearing three drumbeats, 6- to 8-month-old infants preferentially look at a visual display with three objects than at a display with two objects (Starkey, Spelke, & Gelman, 1983, 1990; see also Moore, Benenson, Reznick, Peterson, & Kagan, 1987).

### D3. Adult Subitizing and Estimation

Human adults are fast and accurate at judging the numerosity of small sets of visual objects, a faculty called subitizing (Chi & Klahr, 1975; Kaufman, Lord, Reese, & Volkmann, 1949; Mandler & Shebo, 1982; Taves, 1941). Data from Trick and Pylyshyn (1991), among others, suggest that subitizing is distinct from verbal counting and is a low-level ability of the preattentive visual system. Human adults can also rapidly approximate large numerosities without counting (Klahr & Wallace, 1973; Mandler & Shebo, 1982).

### D4. Animal Numerosity Discrimination

Several animal species can be conditioned to act in a specific way when confronted with a given numerosity (for review see Davis & Pérusse, 1988; Gallistel, 1990). For instance, rats have been conditioned to press one key when a sequence of two tones was presented, and another key when a sequence of four tones was presented (Meck & Church, 1983; Church & Meck, 1984; see also Davis & Albert, 1986, for discrimination of 3 vs. 2 or 4). Such discrimination is not be confined to small numerosities, although it becomes less precise with increasing numerosity (Weber's Law). Thus pigeons have been trained to discriminate sequences of 45 vs. 50 pecks (Rilling & McDiarmid, 1965). Some animals can also be taught to use arbitrary labels, such as arabic digits or verbal labels, to refer to numerosity (Matsuzawa, 1985; Pepperberg, 1987).

### D5. Asymmetry in Generalization

When rats are trained to discriminate between 2 and 8, their indifference point for generalization is not 5 (the arithmetical mean of 2 and 8), but 4 (the geometric mean of 2 and 8) (Church & Meck, 1984).

### D6. Spontaneous Extraction of Numerosity in Animals

Numerosity is often spontaneously extracted by animals. This can be seen in their natural behavior (see Gallistel, 1990 for numerous examples), as well as in more formal conditioning experiments. For instance Meck and Church (1983) conditioned a rat to press one lever in response to a short auditory sequence of two tones, and another lever in response to a longer sequence of eight tones. Duration discrimination was therefore sufficient to succeed in this task. Nevertheless the rats subsequently gave evidence of generalizing on the basis of numerosity alone.

### D7. Cross-Modal Numerosity Discrimination in Animals

A few experiments have demonstrated cross-modal numerosity generalization in animals (for discussion see Davis & Pérusse, 1988). For instance, in Church and Meck's (1984) study, rats were initially trained to press lever A when a sequence of two sounds or two lights was presented, and to press lever B when a sequence of four sounds or four lights was presented. Subsequently

the animals generalized appropriately to the synchronous presentation of sounds and lights.

### D8. Same–Different and Larger–Smaller Relations

The ability to recognize a relation between two numerosities is another elementary numerical faculty that does not depend on language. Fourteen-month-old human infants spontaneously choose the larger of two sets of toys (Sophian & Adams, 1987). In adult animals of several species, spontaneous use of the larger–smaller relation is frequent (e.g., Mitchell, Yao, Sherman, & O'Regan, 1985; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987). In human adults, response time data suggest that arabic numbers are compared by accessing a nonverbal representation of quantities (Moyer & Landauer, 1967). Dehaene and Cohen (1991) found a selective preservation of numerical comparison and other number approximation abilities in a severely aphasic and acalculic patient whose formal calculation abilities were deficient. Such data suggest the persistence, in adult cognition, of elementary comparison and approximation processes, in parallel with more sophisticated language-based calculation abilities (Dehaene & Cohen, 1991; Dehaene, 1992).

### D9. Development of a Linear Ordering

In children, preliminary developmental data suggest that the concept of "same" vs. "different" appears around 10–12 months of age, and the concept of "larger" vs. "smaller" around 14 months of age (Cooper, 1984). In a nonnumerical context, the acquisition of a linear ordering has been studied experimentally in both children and animals (e.g., Bryant & Trabasso, 1971; McGonigle & Chalmers, 1977; von Fersen, Wynne, Delius, & Staddon, 1991). In a typical experiment, the child or animal is first trained on pairs of items (e.g., color rods and random shapes). It is taught to select the appropriate member of the pair: A for the pair A–B, B for the pair B–C, C for the pair C–D, etc. In a second phase generalization is tested with untrained pairs. Choosing for instance B in the pair B–D is interpreted as demonstrating that the subject acquired a linear ordering over the series A–B–C–D–E … and could generalize from B>C and C>D to B>D (transitive inference). Four-year-old children, monkeys, and even pigeons have been shown to pass this test. In addition, von Fersen et al. (1991) have shown that pigeons seem compelled to using a linear representation of the stimuli and cannot acquire a circular order of the form A>B>C>D>A.

### D10. Universality of the Distance Effect

When the numerical distance between two numerosities increases, they become easier to discriminate and can be compared more rapidly. This *distance effect* is a universal characteristic of animal and human elementary number processing abilities (Fig. 1). In pigeons, performance in discrimination of two long sequences of pecks improves as the difference in the number of pecks of the two sequences increases (Rilling & McDiarmid, 1965; Fig. 1A). Chimpanzees have more difficulties choosing the larger of two sets when their numerosities are close in magnitude (Washburn & Rumbaugh, 1991; Fig. 1B). In humans, the time to choose the larger of two numerals, or to decide that two numerals are different, systematically decreases as the numerical distance between the two numerals increases (Moyer & Landauer, 1967; Duncan & McFarland, 1980; Fig. 1C and D). This effect extends to two-digit numerals (Dehaene, 1989; Dehaene, Dupoux, & Mehler, 1990), resists training (e.g., Poltrock, 1989), and is present at 6 years of age, the earliest age
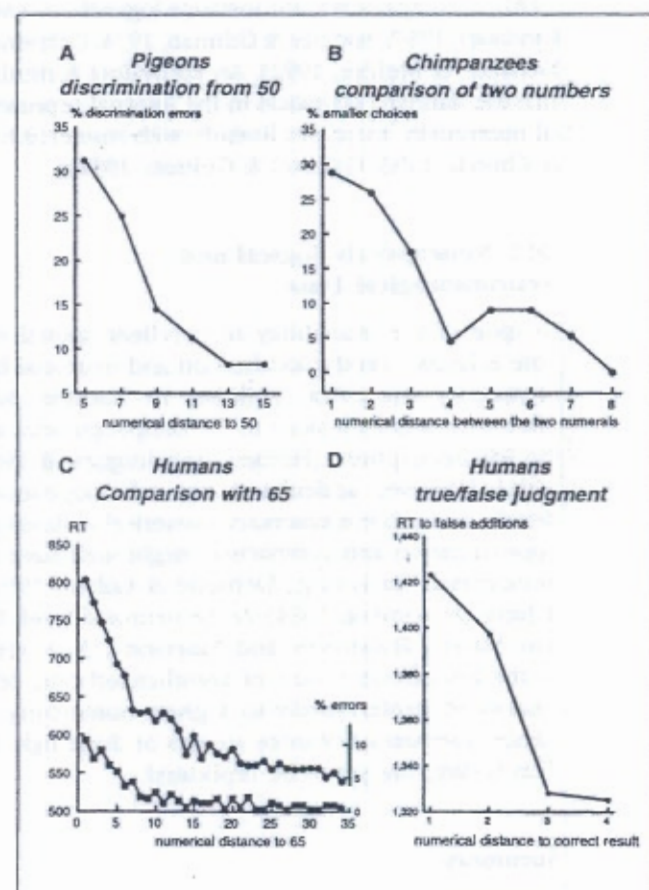


**Figure 1.** Universality of the distance effect. (**A**) Pigeon data, error rate in discriminating between 50 and another numerosity (data from Rilling & McDiarmid, 1965). (**B**) Chimpanzee data, percent choice of the smaller of two arabic numerals (data from Washburn & Rumbaugh, 1991); the chimpanzees were allowed to eat a number of pellets corresponding to the chosen numeral, and preferentially selected the larger number. (**C**) Human data, reaction time and error rate to decide whether a two-digit number is larger or smaller than 65 (data from Dehaene et al., 1990). (**D**) Human data, reaction time to decide if an addition is true or false as a function of the distance from the proposed result to the correct result. (Redrawn from Krueger & Hallford, 1984.)

at which it has been tested (Duncan & McFarland, 1980; Sekuler & Mierkiewicz, 1977).

## D11. Fechner's Law for Numbers

Numerical comparison is more difficult for 8 vs. 9 than for 2 vs. 3, even though the numerical distance is identical in both cases. This decrease of discriminability with larger magnitudes has been observed in animals (e.g., Rumbaugh et al., 1987) as well as in humans (e.g., Buckley & Gillman, 1974; Dehaene, 1989). A variety of psychophysical experiments have indicated that the same objective numerical difference looks subjectively smaller, the larger the numbers against which it is contrasted (for review see Krueger, 1989; Dehaene, 1992). Therefore the suggestion has been made that the internal representation of numerical magnitudes, or number line (Restle, 1970), is compressive, for instance logarithmic (Moyer & Landauer, 1967; Buckley & Gillman, 1974; Dehaene, 1989; Dehaene & Mehler, 1992). An equivalent formulation is that the standard deviation in the internal representation of numerosity increases linearly with numerosity (Meck & Church, 1983; Gallistel & Gelman, 1992).

## D12. Neuropsychological and Neurobiological Data

In spite of the availability of excellent animal models, little is known on the localization and neuronal bases of elementary numerical abilities. In humans, acalculia often results from lesions in the occipitoparietal areas of the left hemisphere (Hécaen, Angelergues, & Houillier, 1961). However acalculia is not a homogeneous syndrome, and more elementary numerical abilities such as approximation and comparison might well have a right-hemispheric basis (e.g., Dehaene & Cohen, 1991; Assal & Jacot-Descombes, 1984). At the neuronal level, Thompson, Mayers, Robertson, and Patterson (1970) recorded, in the association cortex of anesthetized cats, cells that responded preferentially to a given numerosity, for instance, a sequence of three sounds or three light flashes. This finding has yet to be replicated.

## Summary

In brief, we wish to design a formal neuronal model for elementary numerical abilities that would account for (1) the ability to detect visual and auditory numerosities and to represent them internally, (2) the capacity to learn by reinforcement behaviors based on the input numerosity, and (3) the discrimination of numerosity according to a law of increasing difficulty with increasing numerosity (Fechner's Law) and with decreasing distance (distance effect), with a characteristic break around 3 or 4 (subitizing). We shall then show how the addition of another level of neuronal architecture suffices to account for the development of same–different and larger–smaller comparison from a system initially equipped only with numerosity detectors.

## OVERVIEW OF THE FUNCTIONAL ARCHITECTURE OF THE MODEL

We shall first describe the main principles (P) of functional architecture of the model (Fig. 2). A detailed neuronal implementation and a comparison with experimental and neuroanatomical data shall be provided later on.

### P1. The Numerosity Detection System

The first fundamental component of our model is a wired-in *numerosity detection system* comprising three distinct modules: (1) an input *"retina"* on which objects of various sizes and locations can be presented, (2) an intermediate topographical *map of object locations* in which each object, regardless of its size, is represented by a fixed pool of neurons (normalization for size and location), and (3) a map of *numerosity detectors* that sums all outputs from the location map, thereby providing a quantity highly correlated with numerosity and sufficient to approximate it. This architecture solves the computational problem of enumerating objects that may vary widely in size.

We suggest that, in addition to the main input from visual normalization processes, numerosity detectors also receive and combine inputs from an *echoic auditory memory* (Fig. 2). As a result, the numerosity detector for two, for instance, will react identically to two visual objects, to two auditory objects, or to the simultaneous occurrence of one object in both modalities. The numerosity detection system therefore constructs an amodal representation of number.

### P2. Motor Output and Conditioning

We postulate that the numerosity detection system sends numerosity information to a *motor output* system (Fig. 2). The mapping from a given numerosity to a given motor action is learned by selection from an external *reward input*. We assume that the formal organism constantly tries to produce output actions when presented with visual or auditory inputs. Positively rewarded actions are stabilized and negatively rewarded actions are eliminated.

### P3. Development of Same–Different and Larger–Smaller Comparison

The numerosity detection system corresponds to the initial state of human and animal numerical cognition. To account for a subsequent stage of human development during which comparison abilities appear, we introduce
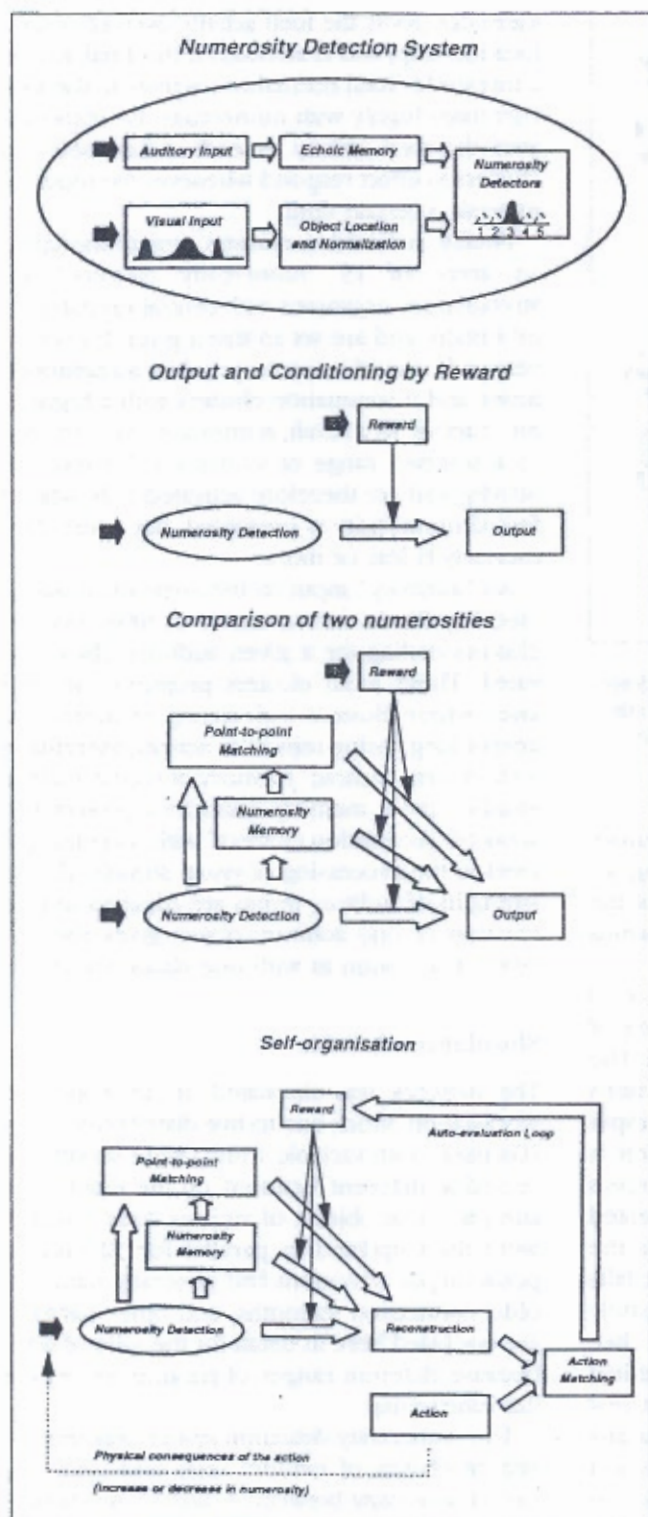
**Figure 2.** Functional description of the proposed model.

present representations. Connections from the memorized and point-to-point matching systems to a motor output module enable the system to learn to react systematically to specific abstract relations between two numerosities. For instance, the system with short-term memory will be able to react to a sequence of two numerosities only when the second is larger than the first, or only when the second is identical to the first.

## P4. Self-Organization of Elementary Numerical Abilities

Human infants do not have to be overtly trained to acquire concepts of "more" or "less." Accordingly, in the most elaborate version of our model, reward is not provided by an external teacher, but is internally generated by a covert *autoevaluation loop* when the system discovers regularities in its environment (Fig. 2). The formal organism "plays" with a set of objects by randomly choosing one of two possible *actions*: adding one object or deleting one object. The ensuing modification of numerosity is noted by the numerosity detection system. On the basis of the memorized and present numerosities, the system attempts to *reconstruct* the selected action. An internal *action-matching module* evaluates the similarity of the reconstructed and actual actions, and sends a positive or negative internal reward signal accordingly. Eventually the system discovers that an increase in numerosity implies addition, and that a decrease implies subtraction.
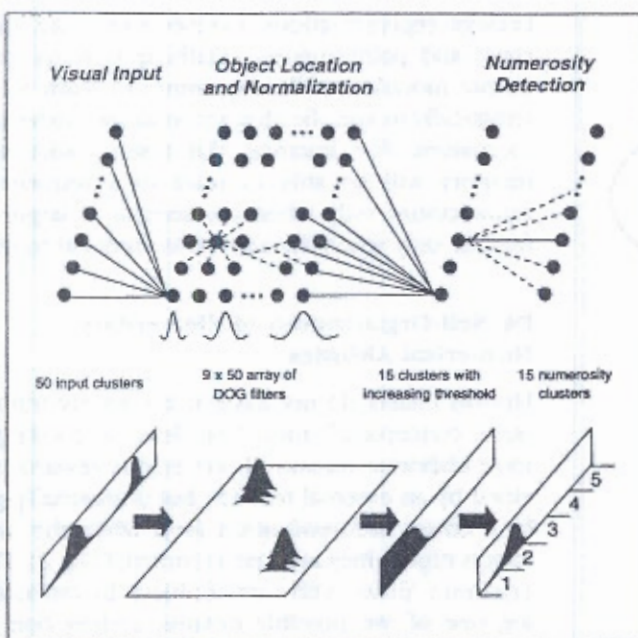
## THE NUMEROSITY DETECTION SYSTEM

The numerical capacities of our model rest mainly on the postulate of wired numerosity detectors that can abstract numerosity independently of the size and arrangement of the input objects. We shall now describe in detail our implementation of the numerosity detection system.

### Network Structure

Figure 3 shows a schematic diagram of the numerosity detection network. For simplicity, physical objects are represented as one-dimensional blobs of various sizes on a simulated "retina." Up to five objects can be presented simultaneously for input. Each object is coded as a local Gaussian distribution of activation over a topographically organized sheet of 50 simulated input neuronal clusters. As in previous publications (Dehaene & Changeux, 1989, 1991; Kerszberg, Dehaene, & Changeux, 1992), each cluster is taken to simulate several hundred or thousand neurons with common response properties, as for instance the cortical "columns" (e.g., Mountcastle, 1978; Goldman-Rakic, 1984). The detailed connectivity and internal activity of a given cluster are not explicitly formalized. Rather, each cluster is implemented as a sin-

an additional *memory module* (Fig. 2). This device permits the temporary maintenance of an active representation of the previous numerosity while a new one is being processed. A point-to-point matching module monitors the points of similarity between the past and

**Figure 3.** Structure and function of the proposed numerosity detection network. Objects of different sizes at the input are first normalized to a size-independent code. Activations are then summed to yield an estimate of input numerosity.

gle McCulloch–Pitts sigmoid unit, with an autoexcitatory connection simulating the various synapses linking individual neurons within each cluster. The output of the unit represents the average number of active neurons within the cluster.

Input clusters project onto a two-dimensional 9 x 50 sheet of neuronal clusters that codes for the location of objects and normalizes for their size (location map). The input connections are set so that each cluster functions as a difference-of-Gaussians (DOG) filter on the input retina. Each of 50 positions for the center of the filter is represented over one dimension of the map, whereas each of 9 possible widths for the filters is represented over the other dimension. As a result, each cluster in the location map reacts preferentially to an object that falls within its receptive field and whose size approximately matches its filter width. Lateral inhibition between clusters that respond to the same or to neighboring retinal locations ensures that after updating activity for a few time steps, only a few clusters will remain active at any position on the location map. In this critical step of object normalization, input objects of different sizes end up being represented by a similar number of active clusters on the location map. The locus of activity merely shifts with object size (Fig. 3). At this stage, object size, which was initially coded by the number of active clusters on the retina (quantity code), is now coded by the position of active clusters on the location map (position code).

Each cluster in the location map projects with equal strength to every unit in an array of 15 clusters with increasing threshold. Each of these "summation clusters"

therefore pools the total activity over all positions of the location map, and is activated if this total activity exceeds a threshold. Total normalized activity in the location map correlates highly with numerosity. By responding whenever the total activity exceeds a threshold, summation clusters in effect respond whenever the input numerosity exceeds a certain limit.

Finally, summation clusters project topographically to an array of 15 "numerosity clusters." Connection strengths are organized with central excitation and lateral inhibition, and are set so that a given numerosity cluster responds only if its corresponding summation cluster is active and if summation clusters with a higher threshold are inactive. As a result, numerosity clusters respond only to a selected range of values for the total normalized activity, and are therefore activated only when their preferred numerosity is presented, not when the input numerosity is less or more.

An "auditory" input to the network is also simulated (see Fig. 2). At each moment in time, one of 15 input clusters coding for a given auditory object can be activated. These input clusters project to an intermediate layer where clusters with strong recurrent connections keep a long lasting remanent activity, therefore providing a short-term "echoic" memory of recent auditory stimuli. Finally echoic memory activations project to the same array of "summation clusters" with increasing thresholds used in the processing of visual stimuli. The connection strengths of auditory inputs are adjusted so that the presentation of one auditory object gives rise to a similar level of activation as with one visual object.

## Simulation Results

The network was simulated on an Appollo DN-10000 workstation. From one to five distributions of activations (Gaussian with variable width) were simultaneously presented at different locations on the input layer, symbolizing a set of objects of various sizes. Cluster activities were then updated in parallel for 12 cycles, at which point output activations had generally stabilized. Thresholds, connection strengths, and other parameter values are not listed here in detail for the sake of simplicity and because different ranges of parameters resulted in similar functioning.

The numerosity detection system was tested with 2500 sets of objects of random sizes and locations (500 for each numerosity between 1 and 5). As shown in Figure 4, repeated presentation of the same numerosity at the input leads to the activation of the same numerosity clusters, regardless of object size and location. Conversely, two distinct numerosities generally activated distinct clusters. Numerosity clusters therefore effectively functioned as detectors of a specific input numerosity (D1, D3, D4). Quite similar results were obtained when auditory objects were presented for input, or when a mixture of visual and auditory inputs was used. Each
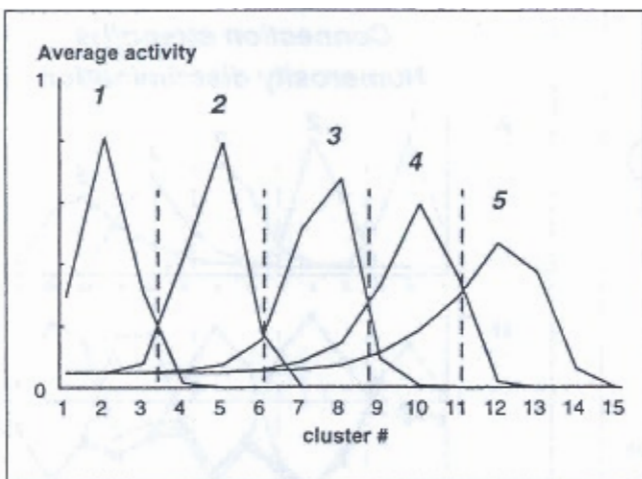
Average activity

**Figure 4.** Average activity of numerosity clusters when random sets of 1, 2, 3, 4, or 5 objects were presented for input. For each input numerosity, only a small number of clusters were selectively activated (e.g., clusters 1, 2, and 3 responded only when a single object was presented). The activity peaks were lower and wider for larger numerosities, implying a decrease in discriminability with increasing numerosity (Fechner's law).

numerosity detector reacted to the total number of objects, regardless of input modality (D2,D7).

The intrinsic variability of our numerosity detection system departs radically from the discrete symbolic representations of number used in digital computers. The activations evoked by different input numerosities often overlapped, implying that the same cluster could be occasionally activated when, say, either three or four objects were presented (Fig. 4). This overlap decreased as the two numerosities became more distant, in agreement with the experimentally observed distance effect (D10). In addition, for equal numerical distance the overlap also increased with numerosity: it was greater between 4 and 5 than between 1 and 2. This property is analogous to the experimentally observed Fechner's law for numbers (D11) and arises from the way numerosity is estimated as a sum of approximately constant activations associated with each input object: the larger the number of terms in the sum, the larger the variance of the result.

## CONDITIONING BY REINFORCEMENT

We have described how a model network can detect numerosity and represent it internally. To simulate behavioral experiments with animals or with infants, we now elaborate further the model to simulate the acquisition of a conditioned behavior. The objective is to condition the simulated organism to select a given output depending on the specific numerosity presented for input.

## Network Structure

A number of output clusters (from two to five depending on the behavioral task) are connected to numerosity detectors via connections of modifiable efficacy. Initially this numerosity-to-output mapping is complete and the connection strengths are set to a small random value. As in our previous simulations (Dehaene & Changeux, 1989, 1991), the strengths are modified according to a Hebbian rule modulated by reward.

$$\delta W_{ij} = (\beta - 1) W_{ij} + \alpha \beta R S_i (2 S_j - 1)$$

where $W_{ij}$ is the connection strength for cluster $i$ to cluster $j$, $S_i$ and $S_j$ are the activities of the pre- and postsynaptic clusters, $\alpha$ is a random variable between 1 and 2, $\beta$ is a relaxation constant, and $R$ is a reward factor between $-1$ and $+1$. The reward $R$ represents another input to the network. Positive values of $R$, which are provided when the performance of the network is correct, have the effect of stabilizing current activity, thereby increasing the chances of selecting the same output again in subsequent trials with the same context. Negative values of $R$, on the contrary, destabilize current activity and therefore favor the selection of a different output on subsequent similar trials.

## Simulation Results

Numerosity discrimination was taught to the network by presenting it with one of two alternative numerosities for input. The formal organism had to produce one type of response when the first numerosity was presented, and another type of response when the second numerosity was presented. When the network failed to activate the appropriate output cluster in response to a given input numerosity, negative reward was sent and the numerosity-to-output connections were modified accordingly.

We trained our network in numerosity discrimination six times with all possible pairs of numerosities between 1 and 5 (1,2; 1,3; 2,3; etc.). Training involved the repeated presentation of stimuli randomly selected from the two possible numerosities, until the network responded correctly on 20 trials in a row. This learning criterion was adopted to provide a simple measure of total learning time, but did not guarantee that optimal performance had been achieved on all stimuli. We therefore checked that further training did not significantly improve performance, enabling us to refer to the percent success after training as the "asymptotic performance."[1]

Figure 5 (top) shows the results for each pair. In all cases it took fewer than 300 trials to reach the learning criterion, and the asymptotic performance after training ranged from 78.5% to 97.8% (D4). Two key aspects of animal and human behavior were reproduced: the distance effect (D10) and the Fechnerian property (D11). As shown in Figure 5 (top), learning was faster and
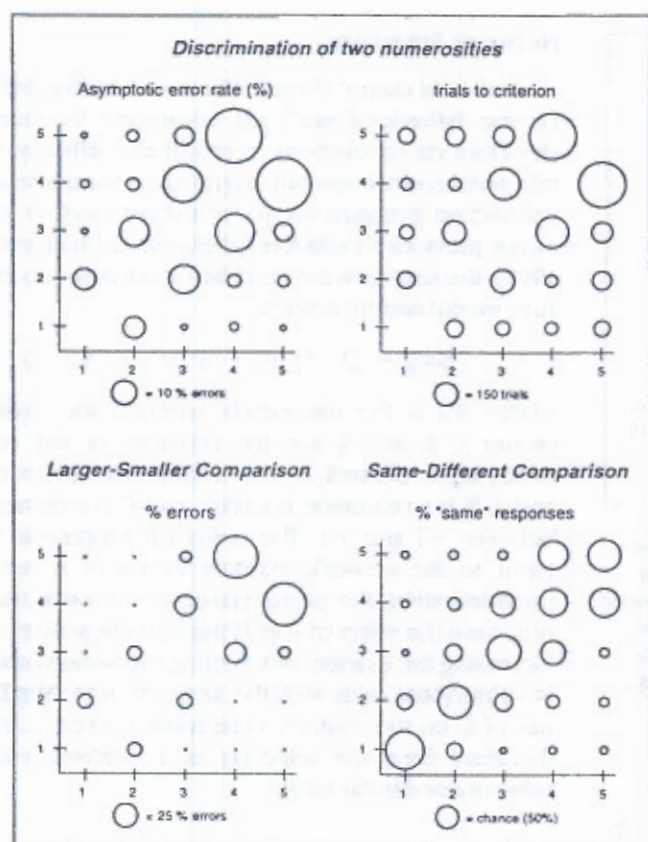
**Figure 5.** Distance effect and Fechner's law in a variety of simulated tasks. Each box gives the network's performance with a given pair of numbers (e.g., the top left circles give the percentage of errors made by the network in discriminating sets of five objects from sets of one object). Off the diagonal, the smaller the circle, the better the performance. The *distance effect* is reflected in the improvement of performance as one moves away from the diagonal. *Fechner's law* is reflected in the degradation of performance with larger and larger numerosities.

asymptotic performance improved with increasing numerical distance between the two discriminated numerosities; and for equal numerical distance, performance was better with small numerosities than with larger ones. The two extremes were the discrimination of 4 vs. 5, which took 285 trials to learn and in which asymptotic performance was 78.5%, versus the discrimination of 1 vs. 4, which took only 81 trials to learn and in which asymptotic performance was 96.8%.

Figure 6C shows the connection strengths after learning numerical discrimination of 2 vs. 4. Numerosity detectors that were often activated when a set of two objects was presented for input developed an excitatory connection with the appropriate output cluster for "2." Likewise, the numerosity detectors for 4 developed an excitatory connection with the other output cluster. These connections were not strictly restricted to the numerosity detectors for 2 and 4, but extended to the neighboring clusters, thus providing robustness and generalization. Indeed our network generalized its response
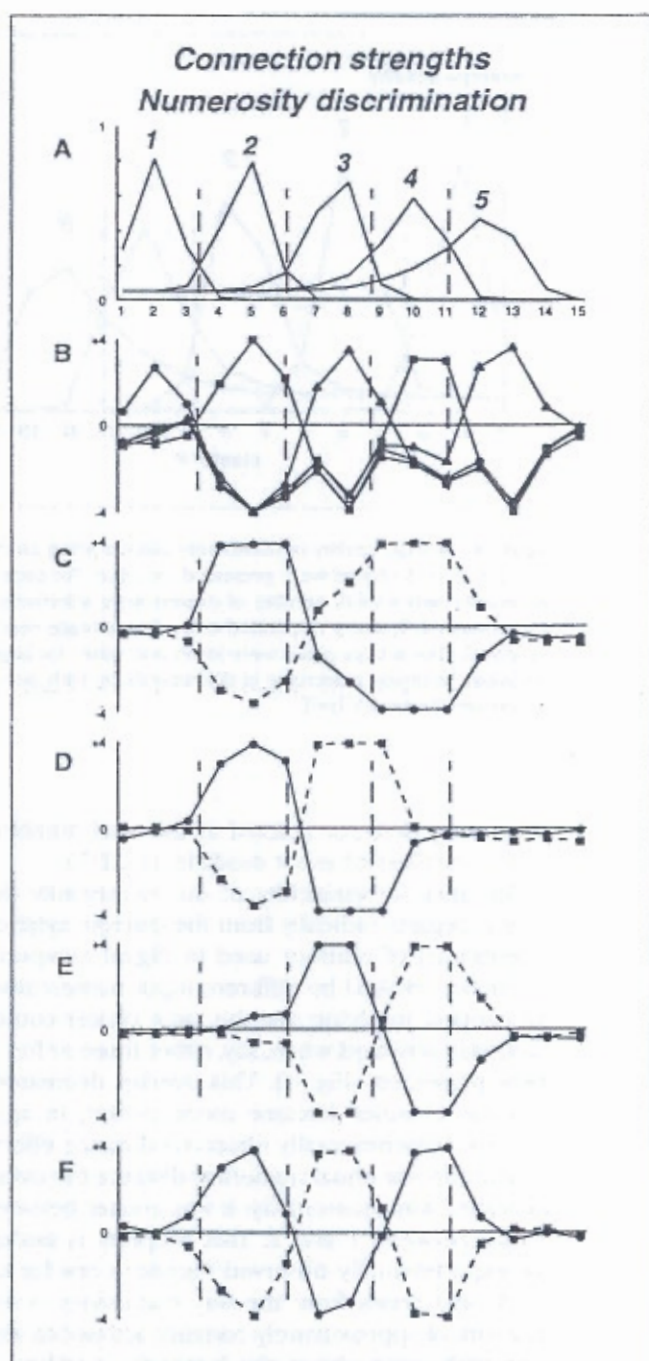


**Figure 6.** Connection strengths after learning various discrimination tasks. The top graph (**A**; same as Fig. 4), used as a reference, gives the average response of the 15 numerosity clusters to numerosities between 1 and 5. Vertical dashed lines group numerosity detectors with the same preferred numerosity. (**B**) Strength of the connections from each of 15 numerosity detectors (abscissa) to each of five output clusters trained to respond only to a given numerosity between 1 and 5. Each output cluster receives excitatory connections only from the adequate numerosity clusters. (**C**) Connection strengths to each of two output clusters in a network trained to discriminate 2 from 4. One output cluster connects mainly to clusters responsive to 2, while the other connects mainly to clusters responsive to 4, with some generalization to 3 and 5. (**D, E, F**) Same as in (**C**), for networks trained to discriminate respectively 2 from 3 (**D**), 3 from 4 (**E**), and 3 from 2 and 4 (**F**).

to 4 when presented with sets of three or five items, and its response to 2 when presented with only one item. Note that generalization was asymmetric (D5): the indifference point between 2 and 4 was displaced to the left of the arithmetical mean (Fig. 6C). As a result, when presented with sets of three items the network mostly made the same response as if four had been presented.

For comparison Figure 6 also shows the synaptic efficacies after the network learned to discriminate 2 from 3 (Fig. 6D) and 3 from 4 (Fig. 6E). Additionally, the network was trained to discriminate 3 from 2 and 4 (D4), with 88.7% success (Fig. 6F). We also simulated a task analogous to Matsuzawa's (1985) or Pepperberg's (1987) experiments (see D4), which required to activate one of five output clusters corresponding to the five possible input numerosities (Fig. 6B). A criterion of 20 successes in a row was reached after 460 trials. The subsequent asymptotic performance was 77.5% correct, but the errors were not randomly distributed over the five possible numerosities. From 1 to 5 the errors rates were respectively 5, 2, 18, 23, and 32%, indicating a decrease of performance with numerosity reminiscent of Fechner's law (D11). For each numerosity, the errors followed a distance effect (D10). For instance when the input numerosity was 5 the network gave the response "4" on 23% of trials, "3" on 7% of trials, and "2" on 1% of trials.

In all such simulations, cross-modal generalization was obtained immediately after training (D2,D7). For instance when trained to discriminate sets of 2 vs. 4 visual objects, the network extended its correct responses to sequences of 2 vs. 4 auditory objects. It also responded adequately to mixtures of auditory and visual objects, for instance, activating the correct output cluster for "4" when presented simultaneously with two visual and two auditory objects (D7).

## SAME–DIFFERENT AND LARGER–SMALLER COMPARISON

Animals and infants are able to choose the larger of two sets (D8). This ability cannot be simulated in the previous model because only one numerosity is processed at any given moment in time. To model numerical comparison, we introduce in this section two novel features: a short-term memory for past numerosity, and a point-to-point matching module for comparing the past and present numerosities.

### Network Structure

Two additional modules are connected between numerosity detectors and output clusters. Both comprise 15 clusters, each corresponding point-to-point to a given numerosity cluster. The first module, labeled *numerosity memory*, consists of clusters with strong autoexcitatory connections enabling them to maintain a sustained level of activity after disappearance of the initial activating

stimulus (see Dehaene & Changeux, 1989, 1991). Numerosity memory clusters receive coarse topographical projections from numerosity detectors, and therefore preferentially memorize the activation level of their corresponding numerosity-detecting cluster. In addition, numerosity memory clusters inhibit each other, thereby ensuring that new stimulation erases old memories. Finally both numerosity detectors and numerosity memory clusters project to all output clusters. These output connections are modifiable according to the above-defined Hebbian rule modulated by reward (Fig. 2).

With this connectivity alone, it is possible for the network to learn a larger–smaller comparison task, i.e., to activate a given output cluster if and only if the second numerosity is larger than the first. This problem is said to be linearly separable and can therefore be learned with the present one-layer architecture (see Appendix for a mathematical demonstration). However this architecture is not sufficient for learning a same–different comparison task, where a given output should be activated if, and only if, the two presented numerosities are identical. Same–different comparison is formally equivalent to the well-known exclusive-OR problem, which cannot be solved with a perceptron architecture (see Appendix). To simulate same–different comparison, another module of *point-to-point matching* clusters is also added. Each point-to-point matching cluster receives coarse topographical projections both from numerosity detectors and from numerosity memory clusters. Thresholds and connection strengths are such that simultaneous activation of a pair of corresponding numerosity-detecting and numerosity-memory clusters is required to activate the associated point-to-point matching cluster. These clusters therefore perform a point-to-point comparison, analogous to a logical AND operation. Strong activity in the point-to-point matching assembly indicates that the present and memorized numerosities are likely to be identical. Again, point-to-point matching clusters project to all output clusters with modifiable strength (Fig. 2).

### Simulation Results
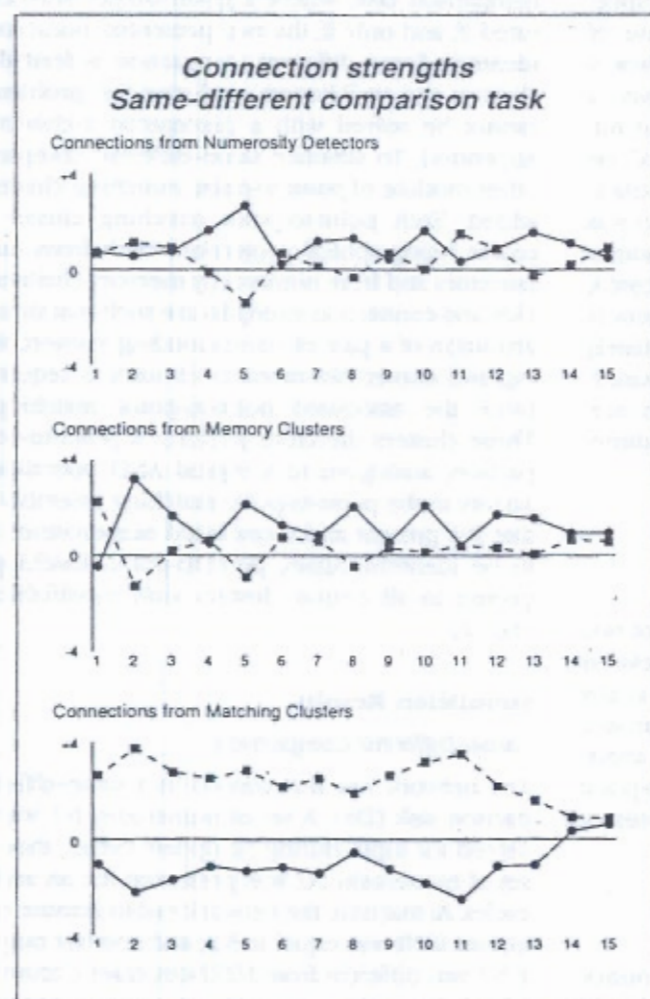
#### Same–Different Comparison

The network was first trained in a same–different comparison task (D8). A set of numerosity N1 was first presented for input during 32 update cycles, then a second set of numerosity N2 was presented for an additional 16 cycles. At that time the network had to activate one output cluster if N1 was equal to N2, and another output cluster if N1 was different from N2 (both cases occurred equally often). Appropriate negative or positive reward was provided and the efficacy of the connections onto output clusters was modified accordingly.

Performance reached 70.3% correct after 300 trials, and did not significantly improve with further training. In spite of this relatively poor global score, two important

effects emerged when the responses to all possible pairs of numerosities were examined (Fig. 5, bottom right). First, performance was affected by a strong distance effect (D10): the more similar the two numerosities, the higher the percentage of "same" responses. For instance the percentage of "same" responses was 85.1% for the pair 1:1, 36.8% for 1:2, and only 15.3% for 1:3. Second, performance decreased with numerosity in a manner reminiscent of Fechner's law (D11). For instance the network responded that 2 and 3 were the same in 38.2% of trials, but it responded that 4 and 5 were the same in 63.5% of trials. The latter percentage was significantly worse than chance ($p < 0.001$) and therefore corresponds to a systematic error of responding "same" when the two compared numerosities were different but numerically close.

Figure 7 shows the connection strengths after learning



**Connection strengths**
**Same-different comparison task**

Connections from Numerosity Detectors

Connections from Memory Clusters

Connections from Matching Clusters

**Figure 7.** Connection strengths after learning the same-different comparison task. Circles and a continuous line indicate connections to the output cluster coding for "different" ($n1 \neq n2$). Squares and a dashed line indicate connections to the output cluster coding for "same" ($n1 = n2$). Note the excitatory connections from matching clusters to the output cluster coding for "same."

the same-different task. All matching clusters tended to activate the output cluster for "same" and to inhibit the output cluster for "different." A "same" response was therefore elicited only when there was activity in the point-to-point matching assembly, signaling a match between the memorized and present numerosities. Conversely, the output cluster for "different" received moderate excitation from numerosity detectors and from memory clusters. This cluster therefore received a constant activation, and was selectively inactivated only when there was activity in the matching assembly.
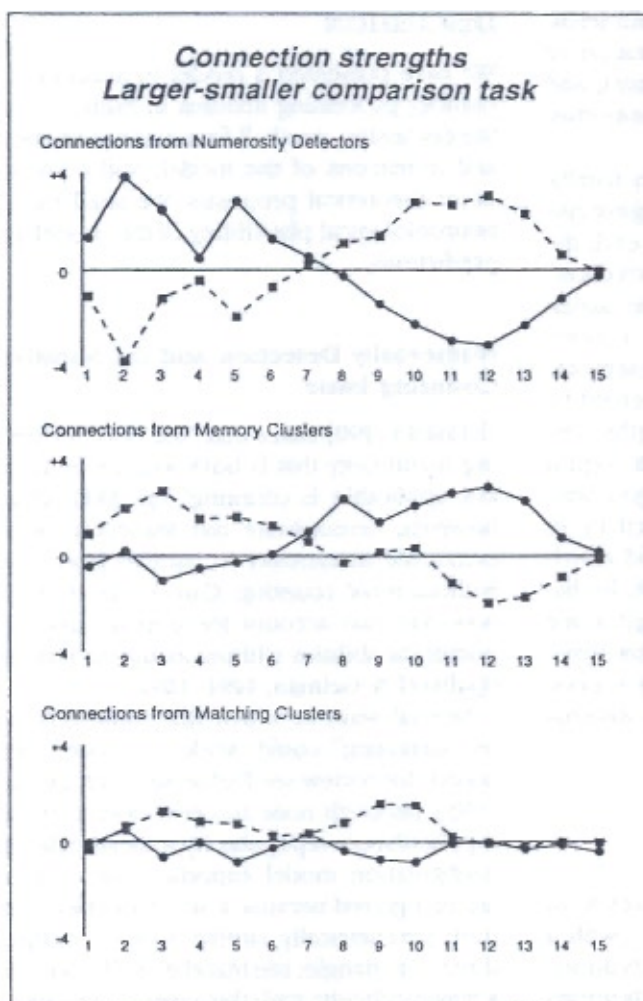
### Larger–Smaller Comparison

Similar inputs were used to train the network in a larger–smaller comparison task (D8). The network had to activate one output cluster if the second numerosity N2 was larger than N1, and another output cluster if N2 was smaller than N1. Both situations were equally frequent, and the situation where N1 is equal to N2 was never presented.

Performance reached an asymptote of 88.9% correct after about 300 trials. Again we found strong distance and Fechnerian effects (D10 and D11; Fig. 5, bottom left). Performance was close to 100% correct for the pairs 1:3, 1:4, 1:5, 2:4, and 2:5. It was much worse for consecutive numerosities, and in that case the percentage of errors was highly affected by numerosity: it ranged from 15% when comparing 1 with 2 to 45% when comparing 4 with 5.

Figure 8 shows the connection strengths that enabled the network to perform larger–smaller comparison. The connections from numerosity detectors to the first output cluster were monotonically increasing with numerosity, whereas for the second output cluster these connections were monotonically decreasing. Exactly the converse was true for connections from memory clusters. The symmetrical pattern of connections from numerosity detectors and from memory clusters enabled each output cluster to perform the equivalent of a subtraction of the two numerosities, and to compare the result of this subtraction with a threshold. In essence, the two output clusters computed the two Boolean functions "N1 − N2 > 0?" and "N2 − N1 > 0?," which are of course equivalent to determining if N1 is larger than N2 or the converse.

It is possible to demonstrate mathematically that the system does not have be presented with all possible pairs of numbers to acquire the larger–smaller relation. It is sufficient that all pairs of consecutive numbers be presented (see Appendix). The system then spontaneously generalizes to pairs of nonconsecutive numbers, therefore accounting for transitive inference experiments (D9).[2] We verified that this property held not only in theory but also in the simulation. After 300 training trials on consecutive pairs only, asymptotic performance tested on all pairs was 88.1% correct. Networks trained on

**Connection strengths**
**Larger-smaller comparison task**

Connections from Numerosity Detectors

Connections from Memory Clusters

Connections from Matching Clusters

**Figure 8.** Connection strengths after learning the larger–smaller comparison task. Circles and a continuous line indicate connections to the output cluster trained to respond only when the memorized numerosity was larger than the present numerosity ($n1 > n2$). Squares and a dashed line indicate connections to the other output cluster ($n1 < n2$). Note the approximately monotonic curves for connection strengths from numerosity detectors and from memory clusters.

consecutive pairs only were indistinguishable from networks trained on all pairs of numbers, and their performance was identical. In particular the distance effect was again reproduced (D10).[3]

We have also simulated a condition similar to the circular test developed by von Fersen et al. (1991), that pigeons were not able to learn (see D9). One output cluster was trained to respond to the ordered pairs 1–2, 2–3, 3–4, 4–5, and 5–1, and the other output cluster was trained to respond when these same pairs were presented in the converse order. The network was never able to attain a satisfactory level of performance on this task (see Appendix for a theoretical account). In the course of learning, a given pair could be classified correctly for a few trials, but on the long run performance never rose beyond the chance level.

## SELF-ORGANIZATION OF ELEMENTARY NUMERICAL ABILITIES

Reinforcement learning, which was used in the above simulations, provides a satisfactory account of conditioning experiments in rats or pigeons. However it cannot explain the spontaneous development, in human and other primates, of an ability to select the larger of two sets in the absence of any training (D8). In this final section we would like to show how an ordering over numerosity detectors (i.e., concepts of "larger" and "smaller") can self-develop without training from an external teacher. We replace the external teacher with an internal autoevaluation loop (Dehaene & Changeux, 1991), which covertly evaluates the performance of the system in representing the effect of additions and subtractions on numerosity.

This concept is best illustrated by an example. Suppose that a child, in the course of playing, adds one block to a set of three blocks and notices that the set now comprises four blocks. There are two ways in which the observation of a regular association between addition, 3, and 4 can be used for the self-organization of numerical abilities. First, the child may learn to predict the effects of addition or subtraction on numerosity (a capacity that we have chosen not to discuss; but see Starkey, 1992; Wynn, 1992).[4] Second, the child may recognize, across different trials, that the relation between 3 and 4 is the same as the relation between, say, 1 and 2. He may thus discover that the ordered pairs, (1,2), (2,3), (3,4), etc., all belong to the same class by virtue of their common association to addition. If the mechanisms that learn this association automatically generalize from consecutive pairs to nonconsecutive pairs, as was shown in the previous section, then this class also extends to any pair in which the first number is smaller than the second. In this manner, the concept of smaller–larger can be acquired.

### Network Structure

The modified network with a capacity for self-organization is shown in Figure 2 (bottom). It was naturally impossible to simulate in any realistic way the motor programs and mental sets that enable a child to "play" with a set of items. Rather, we added two "action" clusters to code for the actions of addition or subtraction of one object. Every 40 update cycles, one of these clusters is activated at random (for a plausible neuronal and molecular implementation of such a "generator of diversity" see Dehaene & Changeux, 1991). The physical effect of the corresponding action is then computed, and one object is added or subtracted to the input set (subject to the constraint that numerosity must remain in the interval 1–5). After a few cycles, this new input pattern yields a new pattern of activation over numerosity detectors. At this stage, the network has the three crucial elements

represented in different assemblies: the initial numerosity is coded in the memory clusters, the operation of addition or subtraction is coded in action clusters, and the resulting numerosity is coded in the numerosity clusters.

The goal of the network is to reconstruct internally, retrospectively, the action that was selected and gave rise to the observed change in numerosity. To this end, the output of the network (now relabeled "reconstruction" in the bottom of Fig. 2) is compared with the actual action that was just performed. If the two match, a covert autoevaluation loop sends positive reward to stabilize the system. The comparison function is implemented by two "action matching" clusters whose strengths and thresholds have been adjusted to implement a logical "AND" operation. "Action matching" clusters project onto the previously defined reward cluster. High activity in the "action matching" assembly indicates a good match between the reconstruction and the actual action. In that case, positive reward is sent and synaptic weights are modified according to the above-defined rule. Low activity among "action matching" clusters indicates a poor match and prompts the sending of a negative internal reward.

### Simulation Results

Starting from a randomly selected input numerosity in the range 1–5, the system was allowed to "play" with a total of 300 additions or subtractions while modifications of connection strengths were allowed. Modifications were then disabled and the system was tested on two sorts of sequential inputs. First it was presented with sequences of consecutive numerosities (e.g., 4 followed by 3) to probe its ability to reconstruct internally the corresponding addition or subtraction operation. The appropriate "reconstruction" cluster was activated in 62.3% of trials, which is significantly better than chance $[\chi^2(1) = 73.9, p < 0.0001]$. Second, the same test was performed with sequences of nonconsecutive numerosities. This time the appropriate "reconstruction" cluster was activated in 74.8% of trials ($p < 0.0001$). For instance when presented with 4 followed by 1, on 99.4% of trials the network figured out that a subtraction operation had been performed. In general the "addition" reconstruction cluster was activated whenever the second numerosity was larger than the first, and the "subtraction" reconstruction cluster was activated whenever the second numerosity was smaller than the first. This demonstrates the self-organization of concepts of "larger" vs. "smaller," or "more" vs. "less," in a system that interacts with sets of objects. The connection strengths developed by this self-organization procedure were similar to those found in the previous section, except for the presence of a higher noise level that resulted in a lower performance level.

## DISCUSSION

We have presented a model to account for elementary number processing abilities in humans and animals. In the discussion, we shall first summarize the main features and limitations of the model, and compare them with other theoretical proposals. We shall then examine the neurobiological plausibility of the model and its testable predictions.

### Numerosity Detection and the Subitizing/Counting Issue

Gallistel (1990) states that "the only process for measuring numerosity that is both well understood and generally applicable is counting" (p. 344). Our simulations, however, demonstrate the feasibility of extracting approximate numerosity in parallel from a visual display, without serial counting. Our model therefore illustrates how one may account for animals' and human infants' numerical abilities without assuming that they can count (Gallistel & Gelman, 1991, 1992).

Several ways in which fast numerosity apprehension or "subitizing" could work have been previously proposed (for review see Dehaene, 1992; Dehaene & Cohen, 1993), although none has ever been turned into a working simulation. A popular hypothesis called the canonical configuration model supposes that small numerosities are recognized because a small number of objects always form geometrically similar spatial configurations (e.g., three = a triangle; see Mandler & Shebo, 1982). However a major difficulty with this view is that subitizing persists even in the absence of any salient geometric information (e.g., with linear arrays; Atkinson et al., 1976). Our model enumerates sets of objects arranged on its one-dimensional "retina" without requiring any particular geometric arrangement of the input set.

Our numerosity detection scheme is not limited to small numbers of objects. However, since the variance in the numerosity estimate increases with numerosity itself (Fechner's law), there is a limit above which two consecutive numerosities cannot be separated. For instance, the performance of the network in the same–different task was close to chance for 3 vs. 4 and for 4 vs. 5 (see Fig. 5, bottom right). We believe that Fechner's law suffices to explain the higher performance of human adults and children with small numerosities, for instance, the fact that 10–12-month-olds are better at discriminating 2 vs. 3 than 3 vs. 4 or 4 vs. 5 (Strauss & Curtis, 1981). There may be no need to postulate a specific process dedicated to the recognition of small numerosities (for discussion, see Dehaene & Cohen, 1993).

In our model, therefore, the variance in the activation induced by each input object plays an important role in explaining several features of numerical processing. Most of this variance is due to the fact that the filters in the location map provide only an approximate match to the

actual size of the input objects. As a result, 2 or 3 location clusters may be activated by each input object. From a biological standpoint, it seems likely that the operation of normalization for size and location cannot be performed with arbitrary precision by real neuronal systems, and that the numerosity estimates derived by the present method will always be variable and obey Fechner's law. Our model predicts, however, that the ability to estimate numerosity may vary between species and/or between individuals of the same species, as a function of the accuracy of their visuospatial normalization routines (Klein & Starkey, 1987).

## Limits of the Numerosity Detection System

The present network suffers from four major limitations:

1. Only up to five objects can be presented for input. This limit is arbitrary and was chosen for computational convenience only. In principle, our scheme allows for the parallel extraction of approximate numerosity from an arbitrarily large set of objects, provided the dimensions of the input retina and the number of numerosity clusters are increased.

2. The input retina is one-dimensional. Our scheme would generalize readily to a two-dimensional retina, provided the object normalization stage was extended to filter two-dimensional blobs of varied sizes.

3. The interaction between the auditory and visual modalities is not modeled beyond the simple summation of numerosities in the two modalities. It seems likely that preverbal organisms can recognize the presence of a single object perceived simultaneously through two modalities. Unlike our model, they would probably not activate "2" if they saw a cow and heard a "moo"! The fusion of auditory and visual modalities into amodal "object files" prior to numerosity detection would be a useful addition to the model.

4. No selection is performed on the nature of the enumerated objects. Our model cannot enumerate, say, only the red items and not the green ones, although there is limited evidence for such behavior in animals (Pepperberg, 1987). An implementation of selective attention is clearly beyond the scope of the present model.

## Development of Numerical Abilities

We have described two major stages in the acquisition of elementary numerical abilities: an initial stage in which only numerosity detection abilities are present, and a second stage, supposedly appearing at the end of the first year of life, in which children become able .o compare two numerosities and to understand ordinality. The transition between these two stages has been described as a learning process in which the system progressively comes to understand how variations in numerosity relate to actions of adding to or subtracting from a set of objects. Initially, the numerosity detectors are not ordered. By exploring the effects of adding or subtracting objets from a set, infants progressively discover the relations between consecutive numerosity detectors. According to Cooper (1984, p. 166), "it is the relationship between the numerosity detector states and the effects of addition and subtraction that give rise to the notions of more and less. From the child's point of view 'more' is invented in this process." Our simulations provide a concrete implementation of these views.

## Limits of Our Developmental Account

Our model is voluntarily restricted to the earliest stages of numerical development. Subsequent important developmental steps that were not considered here include the acquisition of counting (Gelman & Gallistel, 1978), of a lexicon and grammar of number words (Fuson, 1988; Power & Longuet-Higgins, 1978), of an explicit understanding of number conservation (Piaget, 1952), and of arithmetical facts and procedures (Ashcraft, 1992; van Lehn, 1990).

The adult number processing system is likely to be composed of several cognitive layers (Dehaene & Cohen, 1991; Dehaene, 1992), only the most primitive and prelinguistic of which is captured by the present model. Our simulation, for instance, was only 78.5% correct in discriminating 4 vs. 5. While this may actually represent a quantitatively correct evaluation of human performance in speeded discrimination of tachistoscopic stimuli, it is clearly far lower than what humans may achieve under nonspeeded conditions. Likewise, our model was close to chance level in judging which of 4 or 5 is the largest. Normal humans, however, can compare digits with high accuracy, presumably because they possess a number of alternative verbal strategies in addition to the postulated preverbal representation. In general, the present model will be most relevant to experimental situations in which the use of such alternative strategies is prevented, either by experimental design or because verbal processes have been disrupted by a cerebral lesion (e.g., Dehaene & Cohen, 1991).

## Neurophysiological and Neuropsychological Predictions

Our developmental model predicts that elementary numerical abilities rest on two main neuronal networks: the first one, the numerosity detection system, is functional very early in life; the second, which underlies number comparison abilities, develops at the end of the first year. We now consider candidates for the corresponding neuronal structures and outline some testable predictions.[5]

## Numerosity Detection and the Parietal Lobe

We attribute approximate numerosity detection to a parallel process that does not require the serial orientation of visual attention toward each object. The postulate that the numerosity detection system belongs to preattentive vision has been tested and confirmed by Trick and Pylyshyn (1991). For instance, using reaction time methods with normal subjects, they found that the position of the attentional focus had much less influence on subitizing performance than on counting performance, and that factors that influenced preattentive vision also influenced subitizing. Since counting, but not subitizing, requires serial attentional movements to specific locations, our model also predicts that brain-lesioned patients with attentional and/or location specification deficits might have severe difficulties in counting, but no problem with subitizing and estimation. This prediction has recently been borne out in five simultanagnosic patients (Dehaene & Cohen, 1993).

Our model postulates a neuronal *location map* for the parallel extraction of the location and size of visual objects regardless of their exact identity. This role might be subsumed by areas of the parietal lobe, which have been hypothesized to participate in the coding of object location ("where") as opposed to object identity ("what") (Ungerleider & Mishkin, 1982). Extraction of object location and size is necessary to program the adequate motor gesture for grasping an object, a process that critically depends on the integrity of parietal cortex. The initial object normalization stage that we postulate in our model need not be dedicated entirely to numerosity extraction. Rather, its primary use might be the preattentive labeling of object locations for guiding attention and motor behavior. In essence, numerosity estimation would take advantage of an established visuomotor guiding system.

At the neuronal level, a critical prediction of our model concerns the existence of numerosity detectors, or neuronal clusters that respond only to a given input numerosity. Thompson et al. (1970) recorded from five such "counting cells" in the associative cortex of anesthetized cats. However, to our knowledge, the existence of numerosity-detecting cells has not been replicated, perhaps owing to the fact that numerosity is generally not considered as a relevant parameter in cortical activity. We hope that the wide availability of animal models of elementary numerical behavior will prompt a re-evaluation of this notion. Our model tentatively predicts that numerosity-detecting cells should be found within the posterior parietal cortex.

## Number Comparison and the Prefrontal Lobe

To go beyond mere numerosity detection and to model the development of same–different and larger–smaller comparison abilities at the end of the first year of life,

we have had to supplement the initial structure of our network with two neuronal assemblies: one for memorizing past numerosities and another for the point-to-point comparison of the memorized and present numerosities. We would like to suggest that these structural additions correspond to a stage of cortical maturation in which the prefrontal cortex becomes connected to other brain areas. In humans, while numerosity detection is present at birth (Bijeljac et al., 1991; Strauss & Curtis, 1981), the ability to compare two numerosities seems to develop only between 10 and 14 months (Cooper, 1984; Sophian & Adams, 1984). This date fits remarkably well with the known development of delayed-response abilities (Diamond, 1988). Human infants before 9 months of age fail on tests of short-term memory such as Piaget's (1954) A-not-B test or the delayed-response test, even with delays as short as a few seconds. By contrast older infants begin to succeed in the test and after 12 months of age their memory can be sustained over periods of several tens of seconds. In a systematic parallel with the behavior of monkeys, Diamond (1988) showed that adequate performance in delayed-response tasks is critically dependent on the integrity of prefrontal cortex, which gets connected between 9 and 12 months in humans. Neuronal recordings in awake monkeys (Fuster, 1989), as well as modeling studies (Dehaene & Changeux, 1989, 1991), have also confirmed the contribution of prefrontal cortex in the temporary storage, in short-term memory, of a representation of relevant aspects of the external world (Goldman-Rakic, 1987).

Our model shows that numerical comparison also requires the development of similar short-term memory abilities. This parallel between delayed-response and number development, in terms of both time scale and of memory requirements, leads us to postulate a role for prefrontal cortex in the early development of elementary numerical abilities. We predict that number development should be impeded or delayed in infants or in animals with prefrontal lesions. We also predict that cells with long-lasting firing properties, similar to the long-lasting activation of the numerosity memory clusters in our model, may be recorded from the prefrontal cortex of awake animals during numerical comparison tasks.

## CONCLUSION

Although the present model concerned itself only with the early development of numerical abilities, it has broader implications for the nature of cognitive development in humans and animals (Changeux & Dehaene, 1989). First, our work emphasizes the multiple levels of organization that may underlie complex cognitive functions such as number processing. Eventually, the neuronal architectures underlying different levels of cognitive functioning should be untied. Second, we have proposed a general selectionist mechanism for the transition from one level to the next in the course of devel-

opment. For each such transition, we postulate an initial stage of diversification—due, for instance, to the partially stochastic establishment of new connections within a given neuronal architecture—followed by a second stage of selection during which irrelevant connections are pruned and the relevant function is stabilized. The selection operation may be performed by a positive or negative reward signal, which can be either externally imposed, as in many animal conditioning experiments, or covertly generated by the organism itself monitoring its own success via an internal autoevaluation loop (Dehaene & Changeux, 1991). This mechanism departs significantly from Piaget's (1952, 1954) sensorimotor scheme in allowing for internal learning to take place purely by mental experiment, without any overt action of the organism on the external world. Such a process is likely to be critical in mathematical development as well as in other cognitive domains.[6]

## APPENDIX: COMPARISON IN A SINGLE-LAYER NETWORK

This appendix gives some simple mathematical results concerning the learnability of same–different and larger–smaller comparison tasks in a single-layer network of the perceptron type. Consider a network with $2n$ input units with activation $X_1 \ldots X_n$ and $X'_1 \ldots X'_n$, one output unit with activation $A$, and $2n$ connection weights $W_1 \ldots W_n$ and $W'_1 \ldots W'_n$. We assume that the numbers to be compared are coded by single units at the inputs. For instance when a pair of numbers $(n1,n2)$ is presented for input, the activation of input units is

$$X_{n1} = 1 \quad X_n = 0 \quad \text{for } n \neq n1$$
$$X'_{n2} = 1 \quad X'_n = 0 \quad \text{for } n \neq n2$$

The resulting activation $A$ of the output is

$$A = \Phi(W_{n1} + W'_{n2} - T)$$

where $T$ is the threshold of the output unit and $\Phi$ is its input–output function. We assume that $\Phi$ is a strictly increasing function verifying $\Phi(-\infty) = 0$, $\Phi(0) = 0.5$, and $\Phi(+\infty) = 1$. These assumptions are valid for the particular case of the sigmoidal input–output function used in most network simulations.

### Larger–Smaller Comparison

We want the output unit to be active, say, only when $n1$ is strictly larger than $n2$ (other cases can be treated identically). This can be written as

$$\Phi(W_{n1} + W'_{n2} - T) > 0.5 \quad \text{if } n1 > n2$$
$$\Phi(W_{n1} + W'_{n2} - T) < 0.5 \quad \text{if } n1 \leq n2$$

First, we show that it is sufficient to train the network with numbers that are equal or consecutive, and that it will then generalize to all pairs of numbers. Suppose

that the above conditions hold for $n1 = n2$ and for $n1 = n2 + 1$:

$$\Phi(W_{n+1} + W'_n - T) > 0.5$$
$$\Phi(W_n + W'_n - T) < 0.5$$

Letting $Z_n = W_n - T/2$ and $Z'_n = W'_n - T/2$, it follows from the definition of $\Phi$ that

$$Z_{n+1} + Z'_n > 0 \quad \text{and} \quad Z_n + Z'_n < 0$$

This is equivalent to $Z_n < -Z'_n < Z_{n+1}$ for all $n$ (*interlacing condition*). It follows immediately that

$$\text{for all } p \geq 0, \quad Z_n < Z'_{n+p}$$

and

$$\text{for all } p > 0, \quad -Z'_n < Z_{n+p}$$

and these conditions imply that the network responds correctly to all input numbers $n1$ and $n2$.

Note that the actual presentation of cases where $n1$ is equal to $n2$ is vital to the above demonstration. Indeed, suppose that a network had been trained to perform correctly with input pairs (1,2), (2,1), (2,3), and (3,2), but not with the pairs (1,1), (2,2), (3,3), (1,3), and (3,1). Then in some "pathological" cases this network may fail to generalize correctly to the pairs (1,3) and (3,1). In our simulations, however, this pathological situation never occurred.

It is always possible to find connections weights that will satisfy the interlacing condition $Z_n < -Z'_n < Z_{n+1}$ for all $n$. Furthermore, it is easy to reverse the above demonstration and show that the interlacing condition is in fact necessary and sufficient. Larger–smaller comparison is therefore learnable, and learning algorithms such as the delta rule will always find a solution (Minsky & Papert, 1969).

The interlacing condition implies that the weights from the first input are monotonically increasing, whereas the weights from the second input must be monotonically decreasing. This is exactly the pattern of connection weights that was found in our simulation (Fig. 8). This monotonicity of the weights implies a distance effect. The activity $A$ of the output unit will deviate more from its resting level 0.5, the more distant the two compared numbers. This derives directly from the observation that for all $n$,

$$\cdots < W_{n-1} + W'_n - T < W_n + W'_n - T < 0.5 < W_{n+1} + W'_n - T < W_{n+2} + W'_n - T < \cdots$$

and

$$\cdots < W_n + W'_{n+1} - T < W_n + W'_n - T < 0.5 < W_n + W'_{n-1} - T < W_n + W'_{n-2} - T < \cdots$$

For instance if the threshold $T$ is not fixed but subject to noise, as in our simulations, then the probability of an erroneous response will decrease with increasing distance between the two compared numbers. Furthermore if the output unit accumulates activation over time, as is

the case for our self-connected autoexcitatory clusters, then the response time of the unit will also decrease with increasing distance.

## Same–Different Comparison

We now want the output unit to be active, say, only when $n1$ is different from $n2$ (the symmetrical case can be treated identically). This can be written as

$$\Phi(W_{n1} + W'_{n2} - T) > 0.5 \quad \text{if } n1 \neq n2$$
$$\Phi(W_n + W'_n - T) < 0.5 \quad \text{for all } n$$

This problem is similar to the well-known XOR problem and is therefore not learnable in a single-layer perceptron. To demonstrate this, suppose that the four following equations are simultaneously satisfied for a given pair $(n1,n2)$:

$$\Phi(W_{n1} + W'_{n1} - T) < 0.5$$
$$\Phi(W_{n2} + W'_{n2} - T) < 0.5$$
$$\Phi(W_{n1} + W'_{n2} - T) > 0.5$$
$$\Phi(W_{n2} + W'_{n1} - T) > 0.5$$

This is equivalent to

$$Z_{n1} + Z'_{n1} < 0.5$$
$$Z_{n2} + Z'_{n2} < 0.5$$
$$Z_{n1} + Z'_{n2} > 0.5$$
$$Z_{n2} + Z'_{n1} > 0.5$$

The first two equations are clearly incompatible with the two others.

## Acknowledgments

## Notes

1. This level of performance was indeed asymptotic in that it depended only on the representation used for numerosity, and not on the learning algorithm itself. For instance, it was impossible in principle for the network to do better than 80% success in discrimination of 4 vs. 5, because the internal representations of 4 and 5 varied widely and often overlapped.
2. The possibility of accounting for "transitive inference" experiments using classical reinforcement learning, such as the Rescorla–Wagner rule, has been recognized by Couvillon and Bitterman (1992).
3. In transitive inference experiments (D9), the distance effect has an interesting implication: performance is actually lower with the *trained* pairs of consecutive numbers (75.4% correct) than with the *untrained* pairs of nonconsecutive numbers (96.2% correct). Superior performance on untrained pairs has been repeatedly found in transitive inference experiments (e.g., Bryant & Trabasso, 1971; McGonigle & Chalmers, 1977; von Fersen et al., 1991). This counterintuitive observation indicates

that, contrary to what the name "transitive inference" suggests, more distant pairs do not require additional inferential steps. Rather, all pairs, whether trained or untrained, are encoded into the same representation of linear order, the resolution of which improves for larger inter-item distances.
4. Wynn's (1992) results demonstrate knowledge of $1+1$ and $2-1$ in 5-month-old infants. This suggests that the ability to predict the result of additions or subtractions may develop before the ability to compare two numbers, which Cooper (1984) locates around 10–14 months. However contrary to Wynn (1992), we do not think that such data demonstrate the "innateness" of numerical abilities (see Changeux & Dehaene, 1989, for a selectionist approach to the innate/acquired debate).
5. Our discussion of the anatomical bases of numerical abilities focuses on mammals, particularly primates. The anatomical organization of birds is likely to be very different, even though at the computational level their numerical processes might be isomorphic to those of mammals.
6. (Note added in proof.) Anderson and his colleagues (Anderson, Spoehr & Bennett, in press) have proposed a somewhat similar model, with special emphasis on modeling of human adult's arithmetical abilities.

## REFERENCES

Anderson, J. A., Spoehr, K. T., & Bennett, D. J. (in press). A study in numerical perversity: Teaching arithmetic to a neural network. In D. S. Levine & M. Aparicio (Eds.), *Neural networks for knowledge representation and inference*. Hillsdale, NJ: Erlbaum.

Antell, S. E., & Keating, D. P. (1983). Perception of numerical invariance in neonates. *Child Development, 54,* 695–701.

Ashcraft, M. (1992). Cognitive arithmetics: A review of data and theory. *Cognition, 44,* 75–106.

Assal, G., & Jacot-Descombes, C. (1984). Intuition arithmétique chez un acalculique. *Revue Neurologique, 140,* 374–375.

Atkinson, J., Francis, M. R., & Campbell, F. W. (1976). The dependence of the visual numerosity limit on orientation, colour, and grouping in the stimulus. *Perception, 5,* 335–342.

Bijeljac-Babic, R., Bertoncini, J., & Mehler, J. (1991). How do four-day-old infants categorize multisyllabic utterances? Manuscript submitted for publication.

Bryant, P. E., & Trabasso, T. (1971). Transitive inferences and memory in young children. *Nature (London), 232,* 456–458.

Buckley, P. B., & Gillman, C. B. (1974). Comparison of digits and dot patterns. *Journal of Experimental Psychology, 103,* (6), 1131–1136.

Changeux, J. P., & Dehaene, S. (1989). Neuronal models of cognitive functions. *Cognition, 33,* 63–109.

Chi, M. T. H., & Klahr, D. (1975). Span and rate of apprehension in children and adults. *Journal of Experimental Child Psychology, 19,* 434–439.

Church, R. M., & Meck, W. H. (1984). The numerical attribute of stimuli. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition*. Hillsdale, NJ: Erlbaum.

Cooper, R. G. (1984). Early number development: Discovering number space with addition and subtraction. In C. Sophian (Ed.), *Origins of cognitive skills* (pp. 157–192). Hillsdale, NJ: Erlbaum.

Couvillon, P. A., & Bitterman, M. E. (1992). A conventional conditioning analysis of "Transitive Inference" in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 18,* 308–310.

Davis, D. L., & Ashmead, D. H. (1991). *Infants' numerical*

discrimination between sets of sequentially presented figures. Preprint.

Davis, H., & Albert, M. (1986). Numerical discrimination by rats using sequential auditory stimuli. *Animal Learning and Behavior, 14,* 57–59.

Davis, H. & Pérusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence and a new research agenda. *Behavioral and Brain Sciences, 11,* 561–615.

Dehaene, S. (1989). The psychophysics of numerical comparison: A re-examination of apparently incompatible data. *Perception and Psychophysics, 45,* 557–566.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44,* 1–42.

Dehaene, S., & Changeux, J. P. (1989). A simple model of prefrontal cortex function in delayed-response tasks. *Journal of Cognitive Neuroscience, 1,* 244–261.

Dehaene, S., & Changeux, J. P. (1991). The Wisconsin Card Sorting Test: Theoretical analysis and modelling in a neuronal network. *Cerebral cortex, 1,* 62–79.

Dehaene, S., & Cohen, L. (1991). Two mental calculation systems: A case study of severe acalculia with preserved approximation. *Neuropsychologia, 29,* 1045–1074.

Dehaene, S., & Cohen, L. (1993). Neuropsychological dissociation between subitizing and counting in simultaneous patients. (Submitted.)

Dehaene, S., & Mehler, J. (1992). Cross-linguistic regularities in the frequency of number words. *Cognition, 43,* 1–29.

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital: Analogical and symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance, 16,* 626–641.

Diamond, A. (1988). Differences between adult and infant cognition: Is the crucial variable presence or absence of language? In L. Weiskrantz (Ed.), *Thought without language.* Oxford: Clarendon Press.

Duncan, E. M., & McFarland, C. E. (1980). Isolating the effects of symbolic distance and semantic congruity in comparative judgments: An additive-factors analysis. *Memory and Cognition, 8,* 612–622.

Fuson, K. C. (1988). *Children's counting and concepts of number.* New York: Springer-Verlag.

Fuster, J. M. (1989). *The prefrontal cortex* (2nd ed.). New York: Raven.

Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: Bradford Books/MIT Press.

Gallistel, C. R., & Gelman, R. (1991). Subitizing: The preverbal counting mechanism. In W. Kessen, A. Ortony, & F. Craik (Eds.), *Festschrift for George Mandler.* Hillsdale, NJ: Erlbaum.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 44,* 43–74.

Gelman, R., & Gallistel, C. R. (1978). *The child's understanding of number.* Cambridge, MA: Harvard University Press.

Goldman-Rakic, P. S. (1984). Modular organization of prefrontal cortex. *Trends in Neuroscience, 7,* 419–424.

Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational knowledge. In F. Plum & V. Mountcastle (Eds.), *Handbook of Physiology, 5,* 373–417.

Hécaen, H., Angelergues, R., & Houillier, S. (1961). Les variétés cliniques des acalculies au cours des lésions rétrorolandiques: Approche statistique du problème. *Revue Neurologique, 105,* 85–103.

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *American Journal of Psychology, 62,* 498–525.

Kerszberg, M., Dehaene, S., & Changeux, J. P. (1992). Stabilization of complex input-output functions in neural clusters formed by synapse selection. *Neural Networks, 5,* 403–413.

Klahr, D., & Wallace, J. G. (1973). The role of quantification operators in the development of conservation. *Cognitive Psychology, 4,* 301–327.

Klein, A., & Starkey, P. (1987). The origins and development of numerical cognition: A comparative analysis. In J. Sloboda & D. Rogers (Eds.), *Cognitive processes in mathematics* (pp. 1–25). Oxford: Clarendon Press.

Krueger, L. E. (1989). Reconciling Fechner and Stevens: Toward a unified psychophysical law. *The Behavioral and Brain Sciences, 12,* 251–267.

Krueger, L. E., & Hallford, E. W. (1984). Why 2+2=5 looks so wrong: On the odd-even rule in sum verification. *Memory & Cognition, 12,* 171–180.

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General, 111,* 1–21.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature (London), 315,* 57–59.

McCloskey, M. (1992). Cognitive mechanisms in numerical processing: Evidence from acquired dyscalculia. *Cognition, 44,* 107–157.

McGonigle, B. O., & Chalmers, M. (1977). Are monkeys logical? *Nature (London), 267,* 694–695.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 320–334.

Minsky, M., & Papert, S. (1969). *Perceptrons: An introduction to computational geometry.* Cambridge, MA: MIT Press.

Mitchell, R. W., Yao, P., Sherman, P. T., & O'Regan, M. (1985). Discriminative responding of a dolphin (Tursiops truncatus) to differentially rewarded stimuli. *Journal of Comparative Psychology, 99,* 218–225.

Moore, D., Benenson, J., Reznick, J. S., Peterson, M., & Kagan, J. (1987). Effect of auditory numerical information on infant's looking behavior: contradictory evidence. *Developmental Psychology, 23,* 665–670.

Mountcastle, V. B. (1978). An organizing principle for cerebral function: The unit module and the distributed system. In G. M. Edelman & V. B. Mountcastle (Eds.), *The mindful brain.* Cambridge: MIT Press.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgements of numerical inequality. *Nature (London), 215,* 1519–1520.

Pepperberg, I. M. (1987). Evidence for conceptual quantitative abilities in the African grey parrot: Labeling of cardinal sets. *Ethology, 75,* 37–61.

Piaget, J. (1952). *The child's conception of number.* New York: Norton.

Piaget, J. (1954). *The construction of reality in the child.* New York: Basic Books.

Poltrock, S. E. (1989). A random walk model of digit comparison. *Journal of Mathematical Psychology, 33,* 131–162.

Power, R. J. D., & Longuet-Higgins, H. C. (1978). Learning to count: A computational model of language acquisition. *Proceedings of the Royal Society (London), B200,* 391–417.

Restle, F. (1970). Speed of adding and comparing numbers. *Journal of Experimental Psychology, 91,* 191–205.

Rilling, M., & McDiarmid, C. (1965). Signal detection in fixed ratio schedules. *Science, 148,* 526–527.

Rumbaugh, D. M., Savage-Rumbaugh, S., & Hegel, M. T. (1987). Summation in the chimpanzee (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 13,* 107–115.

Sekuler, R., & Mierkiewicz, D. (1977). Children's judgments of numerical inequality. *Child Development, 48,* 630–633.

Sophian, C., & Adams, N. (1987). Infants' understanding of numerical transformations. *British Journal of Developmental Psychology, 5,* 257–264.

Starkey, P. (1992). The early development of numerical reasoning. *Cognition, 43,* 93–126.

Starkey, P., & Cooper, R. G., Jr. (1980). Perception of numbers by human infants. *Science, 210,* 1033–1035.

Starkey, P., Spelke, E. S., & Gelman, R. (1983). Detection of intermodal numerical correspondences by human infants. *Science, 222,* 179–181.

Starkey, P., Spelke, E. S., & Gelman, R. (1990). Numerical abstraction by human infants. *Cognition, 36,* 97–127.

Strauss, M. S., & Curtis, L. E. (1981). Infant perception of numerosity. *Child Development, 52,* 1146–1152.

Taves, E. H. (1941). Two mechanisms for the perception of visual numerousness. *Archives of Psychology, 37,* n° 265.

Thompson, R. F., Mayers, K. S., Robertson, R. T., & Patterson, C. J. (1970). Number coding in association cortex of the cat. *Science, 168,* 271–273.

Treiber, F., & Wilcox, S. (1984). Discrimination of number by infants. *Infant Behavior and Development, 7,* 93–100.

Trick, L. M., & Pylyshyn, Z. W. (1991). A theory of enumeration that grows out of a general theory of vision: Subitizing, counting and FINSTs. University of Western Ontario COGMEM #57.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

van Lehn, K. (1990). *Mind bugs. The origin of procedural misconceptions.* Cambridge, MA: MIT Press.

van Loosbroek, E., & Smitsman, A. W. (1990). Visual perception of numerosity in infancy. *Developmental Psychology, 26,* 916–922.

von Fersen, L., Wynne, C. D. L., Delius, J. D., & Staddon, J. E. R. (1991). Transitive inference formation in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 17,* 334–341.

Washburn, D. A., & Rumbaugh, D. M. (1991). Ordinal judgments of numerical symbols by macaques (*Macaca mulatta*). *Psychologial Science, 2,* 190–193.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature (London), 358,* 749–750.