

The Continuity Between Representations of Small and Large Numbers: A Neural Model

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Abstract

It is debated whether there are two kinds of different numerosity representation systems for small number and large number, respectively. We built a model with the numerosity detector neurons to simulate cognitive process of numerosity representation. Our results are consistent with the electrophysiological data and show the continuity between small and large numbers.

Keywords: Numerosity Representation; Continuity; Neural Model

1. Introduction

It is debated whether there are two kinds of different numerosity representation systems: the precise representation for small number (one to three or four) and approximate representation or analog magnitude representation for large number (larger than three). Feigenson, Dehaene and Spelke (2004) presented two distinct "core systems" of numerical representations which are tuned only to specific types of information in human infants and in other animal species [7]. Kaufman et al. (1949) proposed the concept "subitizing" to denote speedy and exact representation of human adults for small numbers [9]. They found that the response time has little change and error scarcely occurs for small number, conversely, the response time and error are quickly increased for large number. Piazza et al. (2003) indicated that response time and accuracy are discontinuous as increasing numbers [14], which reflected that subitizing and counting are two kinds of processes with different properties.

Results of imaging research provided more direct evidence to the controversy for two systems of numerosity representation. Sathian et al. (1999) reported that subitizing activates foci in the occipital extrastriate cortex, and counting activates a widespread network of brain regions, including large regions of the superior parietal cortex bilaterally and a focus in the right inferior frontal cortex [18]. Piazza et al. (2003) used function MRI to find that the posterior parietal and frontal cortices show a sudden increase in activity only from numerosity four onwards [14]. Nan et al. (2006) indicated the existence of a dichotomy between small number and large number based on the N2 and P3 components of ERP evidence [12]. These

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findings supported the subitizing-counting dichotomy onto separable processes with different functions in the brain.

However, some imaging researches do not agree that the two quantity representation systems have separable neural basis. Some researchers found that subitizing and counting possess common neural basis—the parietal cortex. Piazza et al. (2002) indicated by PET that representation of subitizing and counting both activates extrastriate middle occipital and intraparietal areas (IPS) [15]. Nieder et al. (2002) recorded activity of neurons in the prefrontal cortex and IPS of monkeys for detecting both small and large quantities in the delayed match-to-quantity task [13].

There exist some models for simulating numerosity representation (such as [6], [10] and [19]), which all extend their results to large numbers. However, none of them concerns the question about dichotomy or continuity between small number and large number. In this paper, we will build a model for numerosity representation and do not find discontinuities between representation of small and large numbers.

In section 2, we use a network with both excitatory neurons and inhibitory neurons to explain quantity representation. The connections between neurons are fixed under the hypothesis that basic numerical abilities originate from inheritance. In section 3, the simulation results are compared with the tuning curves of experimental data and do not show any discontinuities between small number and large number. In the last section, we will have a discussion.

2. Model

2.1. Structure

The network is composed of two kinds of neurons: excitatory neurons and inhibitory neurons, whose numbers are N_E and N_I , respectively, with the ratio of 4 : 1 [11]. The network is assumed to encode the identities of p quantity stimuli (corresponding to number 1, 2, ..., p , p is a natural number), each of which activates a distinct and small subpopulation of $f \times N_E$ excitatory neurons, with $f \times p < 1$. Here we set $f \times p = 1/3$, according to the experimental data from [13]. The subpopulation corresponding to number 1 is called subpopulation No.1, the subpopulation corresponding to number 2 is called subpopulation No.2, etc, and the subpopulation of rest $(1 - fp) \times N_E$ neurons is called No. $p + 1$. This classification of excitatory neurons is based on the electrophysiological data from the lateral prefrontal cortex (PFC) of monkeys [13].

The model adopts the network architecture taken from [1], as shown in Figure 1. Each neuron in the network receives C_E excitatory synaptic contacts from excitatory neurons and C_I inhibitory contacts from inhibitory neurons, and C_{ext} excitatory connections transferring noises from outside of the network. Under this structure, every neuron has interactions with all other neurons in the network, and also a feedback to itself.

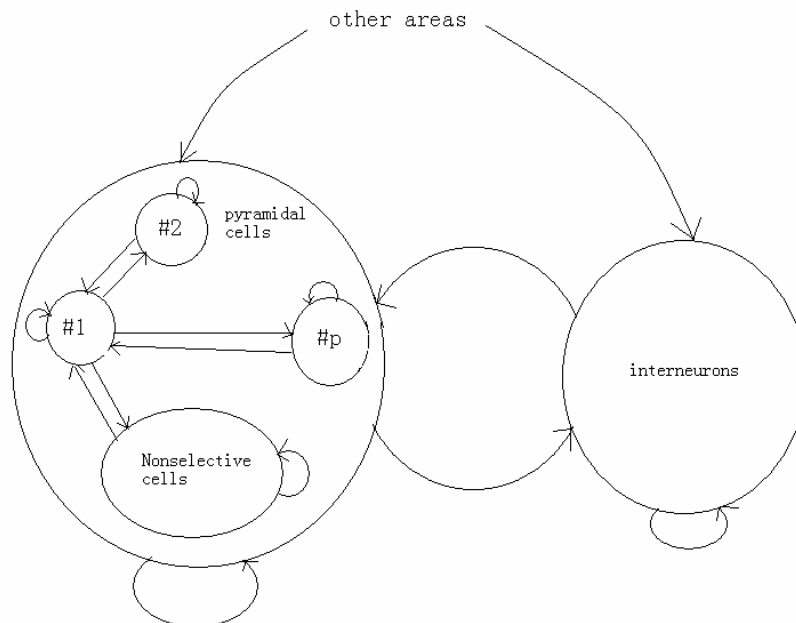


Fig.1 The cortical network. Each neuron in the network is connected to all pyramidal cells by excitatory contacts and all interneurons by inhibitory contacts. They all receive excitatory connections from other cortical areas. The pyramidal cells could be divided into several subpopulations (#1-#p and #p+1), and each of which selectively corresponds to a numerical stimulus, except the subpopulation #p+1. Arrows represent excitatory interactions between neurons, and circles represent inhibitory ones

2.2. Input-output Functions and Weights

The input to the network is as the following protocol: (1) Simulation begins with a pre-cue time interval lasting for 100 ms, during which the network receives only noises. (2) In the stimulus presentation (sample) period, the input consists of quantity stimulus lasting for 400 ms to the selective subpopulations and noises to all neurons. (3) After the quantity stimulus ends, there is a delay period of 100 ms with only noises as input. All the stimuli and noises are encoded by 0-1 binary sequences.

In order to avoid that the numerical selectivity of neurons originates from artificial input to the network, we set all stimuli with the same frequency, despite real input to cortex will be more complex. For one quantity stimulus, the input frequency is set to λ Hz for the corresponding subpopulation and $\lambda/5$ Hz for the other $p-1$ subpopulations. The quantity input to nonselective subpopulation is zero.

Our network has only one layer, hence each neuron both receives input and denotes the output after its state is determined. Assume that each neuron in the network has only two states: $V_i = 1$ (fires a spike) or $V_i = 0$ (no spike) (for pyramidal cells); $V_i = -1$ (fires a spike) or $V_i = 0$ (no spike) (for interneurons).

There is a refractory period $\tau_{rp} = 2$ ms for pyramidal cells, 1 ms for interneurons. When a neuron i is not

in the refractory period, its state V_i varied with time as following arithmetic. For an arbitrary excitatory neuron i , let

$$V_i(t+1) = H(V_i(t) + I_{ee}(t) + I_{ie}(t) + I_{exte}(t) - \theta_e) \quad (1)$$

where $I_{ee}(t) = \sum_{j=1}^{N_E} w_{ji} V_j(t)$ represents excitatory input from all excitatory neurons and

$I_{ie}(t) = \sum_{j=1}^{N_I} w_{ji} V_j(t)$ represents inhibitory input from all inhibitory neurons in the network. $I_{exte}(t)$ is

input from outside, as sum of quantity stimulus and noise.

For an arbitrary inhibitory neuron i , also setting

$$V_i(t+1) = -H(V_i(t) + I_{ei}(t) + I_{ii}(t) + I_{exti}(t) - \theta_i) \quad (2)$$

where $I_{ei}(t) = \sum_{j=1}^{N_E} w_{ji} V_j(t)$ represents excitatory input from all excitatory neurons and

$I_{ii}(t) = \sum_{j=1}^{N_I} w_{ji} V_j(t)$ represents inhibitory input from all inhibitory neurons in the network. $I_{exti}(t)$ is

noise input from outside.

In (1) and (2), H is a Heaviside function, i.e. $H(x) = \begin{cases} 1 & \text{if } x \geq 0 \\ 0 & \text{else} \end{cases}$. θ_e and θ_i are the

thresholds for excitatory and inhibitory neurons, respectively. From the two equations, we know that output of the network is a 0-1 binary matrix.

When neuron i has a connection from neuron j , the connection weight is defined as w_{ji} , which value is fixed in the network for the sake of inheritance hypothesis. The detailed values are seen in table 1. Connection weights between neurons in the same selective subpopulation are set as w_+ . The connection weight between neuron j and neuron i in different selective subpopulations is decided by:

$$w_{ji} = \frac{w_+}{(3 \times |\log_2 n_{post} - \log_2 n_{pre}| + 2)^2} \quad (3)$$

where n_{post} and n_{pre} are the preferred numbers of presynaptic neuron j and postsynaptic neuron i , respectively.

Explicit simulations of the network with several hundred of neurons have been run by Matlab, with integration time step $dt = 0.1$ ms. External spike timings were generated randomly and independently

inside each dt interval.

3. Results

In the simulation, let $N_E = C_E = 300$, $N_I = C_I = 75$, $C_{ext} = 600$. The noises arrive at each external synapse with a rate of 2 Hz, which correspond to a typical value for spontaneous activity in the cerebral cortex [21]. Since there are 600 external synapses, the total background noise to each cell of the network has a rate of $v_{ext} = 1200\text{Hz}$. On the basis of neurophysiological data of neurons in the PFC [13], about 1/3 cells have selectivity for at least one of quantities and other 2/3 cells do not show any significant activation for any of the quantities. Now we set $p = 5$ and $f = 1/15$.

The connection weights are fixed as in table 1, and the strength between different selective subpopulations are computed according to (3).

Table 1 The Values of Weights and Other Parameters in the Model

Meaning of parameters	Values
Weights in the same selective subpopulation (W_+)	0.9
Weights from selective subpopulations to nonselective population	0.1
Weights from nonselective subpopulation to selective populations	0.2
Weights in the nonselective subpopulation	0.1
Weights from excitatory neurons to inhibitory neurons	0.2
Weights from inhibitory neurons to excitatory neurons	0.1
Weights between inhibitory neurons	0.2
Frequency of input (quantity n) to subpopulation No.n (λ)(Hz)	250
Threshold for excitatory neurons	25
Threshold for inhibitory neurons	20

Given input stimuli represented quantities (1 to 5) to the network, we get the results as figure 2. According to firing rates of neurons in figure 2, the network can discriminate output corresponding to different input quantities. These selective neurons have their own preferred quantities corresponding to their peak responses and the neurons have different response for different input quantities. These results are consistent with the experimental data from [13].

In order to evaluate response degrees of selective neurons more justly and exactly, we normalize response activity rates of each subpopulation in the stimulus presentation period using the method of Nieder and his collaborators [13], i.e. neural filter functions of subpopulations are calculated by setting the maximum activity to the most preferred quantity as 100%, and the minimal activity to the least preferred quantity as 0%. The results are as in figure 2. The differences between maximum activity to the most preferred quantity and less activity to the second preferred quantity after subtracting the baselines of each subpopulation are 51%, 60%, 53%, 36%, and 38%, respectively (fig. 2), large enough to distinguish different quantity stimuli.

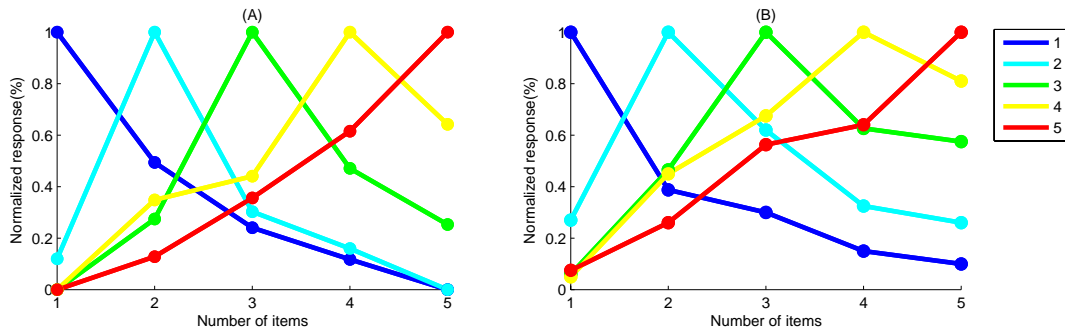


Fig.2 Normalized average activity of selective neurons in the sample period, from our simulation (A) and [13] (B). The activities vary significantly as input quantities. Each neuron exhibits maximal response for one of the five quantities and an orderly drop-off as the quantity progressively varies from the preferred value.

We could change input of the network and find similar results, for example, $p=3$ and $p=9$ as in figure 3. Here, response activity of selective neurons to quantity stimuli is also obviously the function of distance between the most preferred number and others: maximal activity for the most preferred number and decreased activity with increasing distance between numbers. Compared with five input quantities, here decreasing rate of response activity is quicker. If distance between preferred number and input number is more than a certain value (such as three or four), the response rate is relatively small and difference between responses of selective neurons is very small. This distribution of response activity like Mexico hat function reduces burden of neurons, so that a neuron could be merely selective to its preferred quantity and its neighbors.

The results do not find discontinuities between representation of small and large numbers, consistent with several behavioural studies in humans [2], [4], [8] and monkeys [13].

4. Discussion

In this paper we build up a neural network model for continuity of numerosity representation and do not find any discontinuity between representation of small and large numbers. The tuning curves are consistent with the experimental data from [13]. The results show that neurons in the network have characters of numerical selectivity and this property is similar among one-digit numbers. Furthermore, several behavioural studies in humans did not find discontinuities between small and large number representations [2], [4], [8].

The results of the model are consistent with experimental data from [13]. The tuning curves of numerosity-selective neurons have not discontinuity and form a bank of overlapping numerosity filters. The overlapping tuning curves preserve an inherent order of numerosities and do not obviously exhibit cognitive difference between large numbers and small numbers. This is very important because numerosities are different from other sensory stimuli which as isolated categories, but related one another and need the order to be meaningful quantity assignments [20]. Purely sensory stimuli are monotonic function of firing rates with increasing stimulus intensity [17], [3], but numerical stimuli are tuned and overlapping as a type of 'labelled line code' [5].

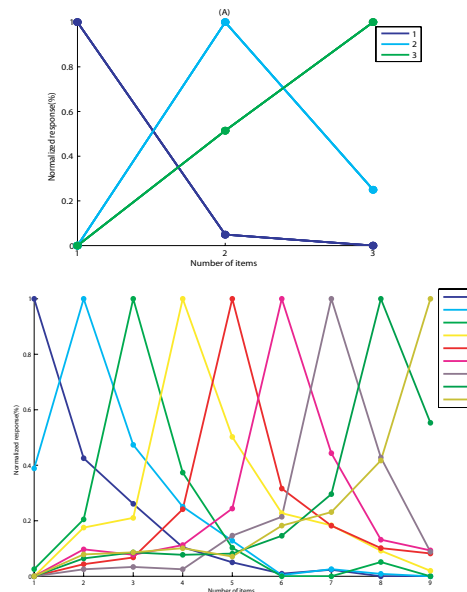


Fig.3 Normalized neural activity of selective subpopulations averaged for neurons in the sample period when input quantities are one to three (A) and one to nine (B), respectively. The parameters are: $N_E = C_E = 180$, $N_I = C_I = 45$, $p = 3$ and $f = 1/9$, threshold for excitatory neurons is 25, (A); $N_E = C_E = 540$, $N_I = C_I = 135$, $p = 9$ and $f = 1/27$, threshold for excitatory neurons is 28, (B); others as figure 2.

Researches by function imaging technology have demonstrated a neural network participating in processing mathematical operations, including the parietal cortex, prefrontal cortex, and cerebellum. It is demonstrated that the neural basis of representation system for large numbers locates in the bilateral horizontal segment of the IPS [6], [16]. However, experimental evidence about the neural basis for small numbers is few. Maybe subitizing is too basic and highly automatic to involve in processing one or more visual stimuli, so that it is hard to search the special basis for subitizing. Therefore, there must be some other mechanisms to supply the imperfection of continuity, as is our future task.

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