Primal categories of neural polarity codes

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Abstract

Neuronal membrane and synapse polarities have been attracting considerable interest in recent years. Certain functional roles for such polarities have been suggested, yet, they have largely remained a subject for speculation and debate. Here, we note that neural circuit polarity codes, defined as sets of polarity permutations, divide into primal-size circuit polarity subcodes, which, sharing certain connectivity attributes, are called *categories*. Two long-debated, seemingly competing paradigms of neuronal self-feedback, namely, axonal discharge and synaptic mediation, are shown to jointly define the distinction between these categories. However, as the second paradigm contains the first, it is mathematically sufficient for complete specification of all categories. The analysis of primal-size circuit polarity categories is found to reveal, explain and extend experimentally observed cortical information capacity values termed “magical numbers”, associated with “working memory”. While these have been previously argued on grounds of psychological experiments, here they are further supported on analytic grounds by the so-called Hebbian memory paradigm. The information dimensionality associated with these capacities is found to be a consequence of prime factorization of composite circuit polarity code sizes. Different categories of circuit polarity, identical in size and neuronal parameters, are shown to generate different firing rate dynamics.

Keywords Primal neural categories · Neural polarity codes · Cortical information capacity · Magical numbers in working memory

Introduction

The state of neuronal activity, contrasted by neuronal silence, has been found to depend on the somatic membrane potential being above or below a certain threshold value (about -60 mV, Melnick 1994). A functional role for the silent neuron has been noted in the 2014 Nobel prize winning work on cortical maps of place (O’Keefe and Dostrovsky 1971; Hafting et al. 2005). The state of synaptic transmissivity, contrasted by synaptic silence, has been found to depend on the value of presynaptic membrane potential, controlled by external stimulation and molecular properties, with respect to a certain threshold value (also about -60 mV, Atwood and Wojtowicz 1999). A detailed biophysical model relates long-term synaptic

potentiation and long-term synaptic depression, which are also viewed in a binary (“bidirectional”) context, to the variable properties and relative numbers of AMPA and NMDA receptors and their external stimulation (Castellani et al. 2001). Localized polarity of membrane and synapse potential with respect to an activation threshold, supported by extensive molecular studies, has been found to control the directional travel of action potentials between neurons (Arimura and Kaibuchi 2005; Kimata et al. 2012; Tanizawa et al. 2006). The effects of neuronal circuit polarity on cortical connectivity, firing dynamics and memory have been analyzed (Baram 2018).

The motivation for the present work is a desire to understand the correspondence between neural circuit connectivity structure and the information it might convey. The underlying structure is shown to be governed by two experimentally supported pairs of paradigms. The first is the above mentioned pair of polarity paradigms, namely, membrane polarity and synapse polarity. The second is the pair of neuronal self-feedback paradigms, namely, the axonal discharge self-feedback paradigm (Carlsson and

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Lindquist 1963; Smith and Jahr 2002) and the synaptically-mediated self-feedback paradigm (Groves et al. 1975). While, from a mathematical viewpoint, the second paradigm is shown to contain the first, their different experimental origins have been associated with different molecular and neurophysiological mechanisms. Formulating the polarities of neuronal membranes and synapses as on–off gates, the polarity code of a fully connected circuit is defined as the set of all neuronal polarity permutations. Employing a mathematical concept used for grouping graphical objects sharing certain attributes (Awodey 2010), we call a neural circuit polarity code, or subcode, sharing a certain substructure, a *category*. In particular, we investigate categories of primal size which, being indivisible, endows the category members with a common characterization. When the circuit polarity code size is not a prime number, the code factorizes into primal-size categories. Circuit of small sizes can interact in a feedforward fashion, arousing relatively large cortical areas. The effects of different neural circuit polarity categories on the neuronal firing rate modes are illustrated by example. The analytically derived neural circuit polarity code and category sizes are found to yield, explain and extend information capacity values experimentally observed in behavioral studies, such as “the magical number seven” (Miller 1956) and “the magical number four” (or, more specifically, “between three and five”, Cowan 2001), associated with so-called “working memory” (Pribram et al. 1960). The dimensionality associated with such capacities is shown to result from prime factorization of composite circuit polarity code sizes. While these have been previously argued on grounds of psychological experiments, here they are further supported on analytic grounds by the so-called Hebbian memory paradigm.

Primal polarity codes and categories under axonal discharge self-feedback

Neuronal membrane and synapse polarities will be described as on–off gates which represent, in the “off” (“disconnect”) position, negative polarity, and, in the “on” (“connect”) position, positive polarity (Baram 2018). Axonal discharge neuronal self-feedback has been observed and its molecular implementation has been specified (Carlsson and Lindquist 1963; Smith and Jahr 2002). The axonal discharge feeds back directly as an input to the neuron, without being further gated by a synapse.

Graphically, the axonal discharge polarity, which is identical to that of the somatic membrane, will be represented by a direct line connecting the neuron’s axon to the neuron’s input. The axonal discharge self-feedback neuron has 2 polarity states, graphically represented by Fig. 1a, b.

Fig. 1 1-category polarity code of primal size 2 of a 1-neuron circuit with axonal discharge self-feedback. While the membrane polarity state is “on” in circuit (a) and “off” in circuit (b), the self-feedback in both circuits is permanently in the “on” state

When the membrane is active (Fig. 1a), so is the axonal discharge self-feedback, and when the membrane is silent (Fig. 1b), there is no self-feedback. As the two states, (a) and (b), are the most elementary polarity patterns under axonal discharge self-feedback, they may be termed the “letters” of the neural circuit polarity code in this context. Yet, as the isolated neuron is also a “1-neuron circuit”, the two polarity states also constitute, in this specific case, 1-letter “words” of the corresponding polarity code. As 2 is a prime number, the two circuits (a) and (b) in Fig. 1 constitute a circuit polarity category. Primality guarantees that a polarity category of n -neuron circuits cannot be divided into smaller subsets having the same number of circuits, unless this number is 1. For instance, the 2-circuit set depicted in Fig. 1 is primal, as, while it divides into 2 subsets, each of these subsets consists of a single circuit. The 1-category polarity code of primal size 7 of a 2-neuron circuit with axonal discharge self-feedback is depicted in Fig. 2.

In order to derive the n -neuron circuit polarity code under axonal discharge self-feedback, it is first noted that there can be up to n active neurons (neurons with positive membrane polarities) and $n(n-1)$ synapses. A synapse can be either active or silent. It follows that there can be up to

Fig. 2 The primal-size 7-word polarity code constituting a single category of 2-neuron circuits under axonal discharge self-feedback

$$P^{(1)}(n) = 2^{n(n-1)} \quad (1)$$

different circuits involving only active membranes and possibly silent synapses. In addition, there can be up to

$$P^{(2)}(n) = \binom{n}{1} + \binom{n}{2} + \cdots + \binom{n}{n} = 2^n - 1 \quad (2)$$

circuits with silent neurons (counting all permutations of 1 silent neuron, 2 silent neurons, ..., n silent neurons out of n neurons). Note that the circuits corresponding to the active states of these neurons were already counted in $P^{(1)}(n)$, so that the only additional circuits are the same ones with these neurons silenced. It follows that there is a maximum total of

$$P(n) = P^{(1)}(n) + P^{(2)}(n) = 2^{n(n-1)} + 2^n - 1 \quad (3)$$

different circuits, constituting the size of the circuit polarity code of n axonal discharge self-feedback neurons.

Equation 3 yields $P(1) = 2$, $P(2) = 7$, $P(3) = 71$ and $P(4) = 4111$. Employing methods of primality verification, e.g., the Miller-Rabin method (Miller 1976; Rabin 1980), it can be verified that $P(1), P(2), P(3)$ and $P(4)$ are all prime numbers (they are the 1st, the 4th, the 20th, and the 566th prime numbers, not counting 1). On the other hand, $P(5) = 1,048,607$, $P(6) = 1,073,741,887$ and $P(7) = 4,398,046,511,231$ are not prime. As the prime factorization of 1,048,607 is $7 \times 59 \times 2539$, the polarity code of 5-neuron circuits factorizes into $7 \times 59 = 413$ categories of primal size 2539, or $7 \times 2539 = 17,773$ categories of primal size 59, or $59 \times 2539 = 149,801$ categories of primal size 7. As the prime factorization of 1,073,741,887 is $37 \times 109 \times 266,239$, the polarity code of 6-neuron circuits factorizes into $37 \times 109 = 4251$ categories of primal size 266,239, or $37 \times 266,239 = 9,850,843$ categories of primal size 109, or $109 \times 266,239 = 29,020,051$ categories of primal size 37. As the prime factorization of 4,398,046,511,231 is $163 \times 15,451 \times 1,746,287$, the polarity code of 7-neuron circuits factorizes into $163 \times 15,451 = 2,518,513$ categories of primal size 1,746,287, or $163 \times 1,746,287 = 284,644,781$ categories of primal size 15451, or $15451 \times 1,746,287 = 26,981,880,437$ categories of primal size 163. Our attempts to derive the prime factorization of the polarity code sizes corresponding to n -neuron circuits for $n \geq 8$ have failed, as the term $2^{n(n-1)}$ in Eq. 3 becomes exceedingly dominant with respect to the other terms, erroneously producing powers of 2 (specifically, $2^{n(n-1)}$) as “prime factors” of $P(n)$. In contrast to the single primal polarity code sizes corresponding to circuits of 1–4 neurons, which may be characterized as having a single dimension, the three different primal polarity category sizes corresponding to circuits of 5, 6 and 7 neurons may be characterized as

representing three different dimensions. Composite numbers that factorize into three prime numbers have been called *sphenic numbers*. Such numbers have been addressed in purely mathematical contexts (Lehmer 1936) and their natural relevance appears to be noted here for the first time.

The entire code of an n -neuron circuit polarity under axonal discharge self-feedback can be cortically represented by $P(n)$ circuits. For instance, the 7-circuit group of 2-neuron circuits depicted in Fig. 2 represents the corresponding 7 different polarity code words under axonal discharge self-feedback. The implementation of the polarity code of a 1-neuron circuit would require then $1 \times 2 = 2$ neurons, while the implementation of the polarity code of a 2-neuron circuit would require $2 \times 7 = 14$ neurons. The implementation of the polarity codes of 3 and 4-neuron circuits would require $3 \times 71 = 213$ and $4 \times 4111 = 16,444$ neurons, respectively. The implementation of the polarity codes of 5 and 6-neuron circuits would require $5 \times 1,048,607 = 5,243,035$ and $6 \times 1,073,741,887 = 6,442,451,322$ neurons, respectively. The implementation of a 7-neuron circuit polarity code, having size $P(7) = 4,398,046,511,231$ would require $7 \times 4,398,046,511,231 = 30,786,325,578,617$ neurons, far exceeding the number of neurons in the human brain (10^{12}). However, it should be noted that any fraction of a polarity code, including such codes corresponding to circuits of n neurons where $n \geq 7$, is implementable by a number of categories smaller than the one calculated for the full implementation of the polarity code. For instance, if only half the number of neurons needed for a full implementation of the 7-neuron polarity code are available, half the number of categories in each of the three corresponding sphenic subgroups of categories would be implementable.

Table 1 summarizes the circuit sizes, the corresponding circuit polarity code sizes, the polarity code size prime factorization, the numbers of primal-size categories, and the corresponding primal category sizes for circuits of 1–7 neurons. The polarity code sizes of 5, 6 and 7-neuron circuits are factorized as specified above.

Polarity codes and categories under synaptic self-feedback

Neuronal self-feedback, employing an intermediate synapse between axonal output and neuronal input, has been suggested (Groves et al. 1975) as an alternative to direct axonal discharge self-feedback without synaptic mediation (Carlsson and Lindquist 1963; Smith and Jahr 2002). In contrast to axonal discharge self-feedback, under the synaptic self-feedback paradigm, each of the circuit

Table 1 Neural circuit polarity code sizes for circuit sizes 1–7 under axonal discharge self-feedback

# of circuit neurons	Polarity code size	Polarity code size prime factorization	# of primal-size categories	Primal category size
1	2	2	1	2
2	7	7	1	7
3	71	71	1	71
4	4111	4111	1	4111
5	1,048,607	$7 \times 59 \times 2539$	413	2539
			17,773	59
			149,801	7
6	1,073,741,887	$37 \times 109 \times 266,239$	4251	266,239
			9,850,843	109
			29,020,051	37
7	4,398,046,511,231	$163 \times 15,451 \times 1,746,287$	2,518,513	1,746,287
			284,644,781	15,451
			26,981,880,437	163

The polarity category sizes are primal, 2, 7, 71 and 4111, respectively, for circuits of 1–4 neurons, and sphenic (3-prime factorizable) for circuits of 5, 6 and 7 neurons

neurons has a self-synapse that can be in one of the two polarity states: “on” or “off”. It follows that there are

$$C(n) = \binom{n}{0} + \binom{n}{1} + \cdots + \binom{n}{n} = 2^n \quad (4)$$

permutations of self-feedback polarity states in a circuit of n neurons. The total polarity code size for an n -neuron circuit is then

$$Q(n) = C(n)P(n) \quad (5)$$

where $P(n)$ is the polarity code size of n -neuron circuits under the axonal discharge feedback paradigm, represented by Eq. 3. Specifically, for $n = 1$ we have $C(1) = 2$, hence, $Q(2) = 2 \times 2 = 4$. For $n = 2$ we have $C(2) = 4$, hence, $Q(2) = 4 \times 7 = 28$. For $n = 3$ we have $C(3) = 8$, hence, $Q(3) = 8 \times 71 = 568$, and for $n = 4$ we have $C(4) = 16$, hence, $Q(4) = 16 \times 4111 = 65,776$. For $n = 5$ we have $C(5) = 32$, hence, $Q(5) = 32 \times 1,048,607 = 33,555,424$, and for $n = 6$ we have $C(6) = 64$, hence, $Q(6) = 64 \times 1,073,741,887 = 68,719,480,768$. For $n = 7$ we have $C(7) = 128$, hence, $Q(7) = 128 \times 4,398,046,511,231 = 562,949,953,437,568$. Similarly, for each of the primal-size categories of n -neuron circuits with $n = 5$, $n = 6$ and $n = 7$, produced by prime factorization under the axonal discharge self-feedback paradigm, there are $C(n)$ such categories associated with the permutations of the polarity states corresponding to synaptic self-feedback.

The 4-circuit polarity code for a single neuron under the synaptic self-feedback paradigm is displayed in Fig. 3, where the two categories of primal size 2 each are represented by columns (a) and (b). The 4 circuit polarity

categories of 7 circuits of 2 neurons each are displayed in Fig. 4. It can be seen that the first category, represented by column (a), is the category corresponding to axonal discharge self-feedback, hence both neurons’ self-synapses being in the “on” state, as derived in the previous section and depicted in Fig. 2. The second category, represented by column (b), corresponds to the left neuron’s self-synapse being in the “off” state, while the right neuron’s self-feedback is in the “on” state. The third category, represented by column (c), corresponds to the right neuron’s self-synapse being in the “off” state, while the left neuron’s self-feedback is in the “on” state. The fourth category, represented by column (d) corresponds to both neurons’ self-synapses being in the “off” state.

For each of the primal-size categories of n -neuron circuits under axonal discharge self-feedback there are $C(n)$

Fig. 3 The 2-circuit categories, represented by columns **a** and **b**, of 1-neuron polarity code under synaptic self-feedback. Category (a) is identical to the 1-category polarity code of a single neuron under axonal discharge feedback, depicted in Fig. 1

Fig. 4 The 7-circuit categories of 2-neuron circuit polarity code represented by the 4 columns: **a** both self-synapses are “on”, **b** left neuron’s self-synapse is “off” and right neuron’s self-synapse is “on”, **c** left neuron’s self-synapse is “on” and right neuron’s self-synapse is “off”, **d** both self-synapses are “off”

primal-size categories under synaptic self-feedback. It follows that for circuits of 1, 2, 3 and 4 neurons there are 2, 4, 8 and 16 categories of primal sizes 2, 7, 71 and 4111, respectively. Employing the polarity code size prime factorization numbers under axonal discharge self-feedback displayed in Table 1, for circuits of 5 neurons there are $32 \times 413 = 13,216$ categories of primal size 2539, or $32 \times 17,773 = 568,736$ categories of primal size 59, or $32 \times 149,801 = 4,739,632$ categories of primal size 7. For circuits of 6 neurons there are $64 \times 4251 = 272,064$ categories of primal size 266,239, or $64 \times 9,850,843 = 630,453,952$ categories of primal size 109, or $64 \times 29,020,051 = 1,857,283,264$ categories of primal size 7. For circuits of 7 neurons there are $128 \times 163 \times 15451 = 322,369,664$ categories of primal size 1,746,287, or $128 \times 163 \times 1,746,287 = 36,434,531,968$ categories of primal size 15451, or $128 \times 15451 \times 1,746,287 = 3,453,680,695,936$ categories of primal size 163. As in the case of axonal discharge self-feedback, the three different primal polarity category sizes obtained by factorization of the non-primal (sphenic) polarity code sizes corresponding

to circuits of 5, 6 and 7 neurons may be characterized as representing three different dimensions.

The entire code of an n -neuron circuit polarity under synaptic self-feedback can be cortically represented by $Q(n)$ circuits. Consequently, the implementation of the polarity code of 1 and 2-neuron circuits would require $2 \times 2 = 4$ and $2 \times 28 = 56$ neurons, respectively. Accordingly, the implementation of the polarity codes of 3, 4, and 5-neuron circuits would require $3 \times 568 = 1,704$, $4 \times 65,776 = 263,104$ and $5 \times 39,135,393 = 167,777,120$ neurons, respectively. The implementation of the polarity code of 6-neuron circuits would require $6 \times 75,418,890,625 = 452,513,343,750$ neurons, and the implementation of the polarity code of 7-neuron circuits would require $7 \times 562,949,953,437,568 = 3,940,649,674,062,976$ neurons, far exceeding the number of neurons in the human brain (10^{12}). However, as in the case of axonal discharge self-feedback, it should be noted that any fraction of a polarity code, including such codes corresponding to circuits of n neurons where $n \geq 7$, is implementable by a number of categories smaller than the

Table 2 Neural circuit polarity code and category sizes for circuits of 1–7 neurons under synaptic self-feedback

# of circuit neurons	# of self-synapse polarity permutations	Circuit polarity code size	# of primal-size categories	Primal category size
1	2	4	2	2
2	4	28	4	7
3	8	568	8	71
4	16	65,776	16	4111
5	32	33,555,424	13,216	2539
			568,736	59
			4,739,632	7
6	64	68,719,480,768	272,064	266,239
			630,453,952	109
			1,857,283,264	37
7	128	562,949,953,437,568	322,369,664	1,746,287
			36,434,531,968	15,451
			3,453,680,695,936	163

The polarity category size is primal, 2, 7, 71 and 4111, respectively, for circuits of 1–4 neurons, and sphenic for circuits of 5, 6 and 7 neurons

one calculated for the full implementation of the corresponding polarity code.

Table 2 summarizes, for circuits of 1–7 neurons, the number of self-synapse polarity permutations, the circuit polarity code size, the number of primal-size polarity categories, and the corresponding primal category sizes.

Neural circuit polarity effects on firing dynamics

We now consider the effect of neural circuit polarity on its firing rate dynamics. In particular, we examine the expression of different circuit polarity categories, implying different circuit connectivity patterns, by different firing rate modes. We assume synaptic self-feedback, which, as explained in the previous section, contains axonal discharge self-feedback as a mathematical subcategory.

The neuronal firing model has evolved from the integrate-and-fire (Lapicque 1907) and the conductance-based membrane current (Hodgkin and Huxley 1952) paradigms, through cortical averaging (Wilson and Cowan 1972) and neuronal decoding (Abbott 1994) to the spiking rate model (Gerstner 1995)

$$\tau_{m_i} \frac{d}{dt} v_i(t) = -v_i(t) + f_i \left(\mathbf{w}_i^T(t) \int_{-\infty}^t e^{-(t-\sigma)/\tau_i} \mathbf{v}_i(\sigma) d\sigma + u_i(t) \right) \quad (6)$$

where $v_i(t)$ is the firing rate of the i 'th neuron, τ_{m_i} is the corresponding membrane time constant, $\mathbf{v}_i(t)$ is the vector

of firing rates of the circuit's pre-neurons of the i 'th neuron, $\mathbf{w}_i$ is the corresponding vector of synaptic weights, τ_i is the synaptic time constant, $u_i(t)$ is the membrane activation potential, $u_i(t) = I_i(t) - r_i(t)$, with $I_i(t)$ an external input potential and $r_i(t)$ the membrane activation threshold (approximately -60 mV), and where

$$f_i(x) = f(x) = \begin{cases} x & \text{if } x \geq 0 \\ 0 & \text{if } x < 0 \end{cases} \quad (7)$$

is the conductance-based rectification kernel (Carandini and Ferster 2000), first observed in empirical data (Granit et al. 1963; Connor and Stevens 1971).

It has been noted that the mathematically imposing integral term in Eq. 6 is biologically and functionally insignificant (Wilson and Cowan 1972), and that the essence of neural firing dynamics is captured by its instantaneous manifestation (see, e.g., Dayan and Abbott 2001; Miller and Fumarola 2012), yielding the firing rate model

$$\tau_{m_i} \frac{d}{dt} v_i(t) = -v_i(t) + f_i(\mathbf{w}_i^T(t) \mathbf{v}_i(t) + u_i(t)) \quad (8)$$

The BCM plasticity rule (Bienenstock et al. 1982), enhanced by stabilizing modifications (Intrator and Cooper 1992; Cooper et al. 2004), is a widely recognized, biologically plausible, mathematical representation of the Hebbian learning paradigm (Hebb 1949). It suggests the computation of $\mathbf{w}_i(t)$ by the model

$$\tau_{\omega_i} \frac{d}{dt} \mathbf{w}_i(t) = -\mathbf{w}_i(t) + (v_i(t) - \theta_i(t)) \mathbf{v}_i^2(t) \quad (9)$$

where τ_{ω_i} is the learning time constant and $\theta_i(t)$ is a

variable threshold satisfying (Intrator and Cooper 1992; Cooper et al. 2004)

$$\theta_i(t) = \frac{1}{\tau_{\theta_i}} \int_{-\infty}^t v_i^2(\tau) \exp(-(t-\tau)/\tau_{\theta_i}) d\tau \quad (10)$$

where τ_{θ_i} is the thresholding time constant.

The discretization of a continuous-time dynamical system (e.g., Qwakenaak and Sivan 1972) is done under the assumption that the time steps are sufficiently small so as to allow the approximation of the input by a constant value throughout the time step. Such approximation may, in principle, introduce inaccuracies in the description of the system's behavior, yet, discretization is often used as computational means as long as it does not introduce instability. In the present context of neural behavior, the validity of the discrete time model can be qualitatively tested by comparison of simulations to the ample evidence produced by neurobiological experiments. The discrete time versions under unity time steps of Eqs. 8–10 are

$$v_i(k) = \alpha_i v_i(k-1) + \beta_i f(\omega_i^T(k) v_i(k-1) + u_i) \quad (11)$$

$$\omega_i(k) = \varepsilon_i \omega_i(k-1) + \gamma_i [v_i(k-1) - \theta_i(k-1)] v_i^2(k-1) \quad (12)$$

$$\theta_i(k) = \delta_i \sum_{i=0}^N \exp(-i/\tau_{\theta_i}) v_i^2(k-i) \quad (13)$$

where $\alpha_i = \exp(-1/\tau_{m_i})$, $\beta_i = 1 - \alpha_i$,

$\varepsilon_i = \exp(-1/\tau_{\omega_i})$, $\gamma_i = 1 - \varepsilon_i$, and $\delta_i = 1/\tau_{\theta_i}$.

Since, as we have shown, circuit polarity categories grow exponentially with the number of circuit neurons, we limit our simulations of firing rates to circuits of two neurons. Employing the parameter values

$$\begin{aligned} \tau_{m_1} = \tau_{m_2} = 5, \tau_{\omega_1} = \tau_{\omega_2} = 0.1, \tau_{\theta_1} = \tau_{\theta_2} = 0.1, u_1 = u_2 \\ = 5 \text{ with } v_1(0) = v_2(0) = 0 \end{aligned} \quad (14)$$

we have simulated categories a–d in Fig. 4. The results are shown in Figs. 5, 6, 7 and 8, where v_1 and v_2 represent the firing rate sequences of the two circuit neurons in each of the cases. Each of the pairs v_1 and v_2 should be viewed in the context of the corresponding circuit depicted in Fig. 4. The details of each of the four categories are specified in the corresponding figure captions. It can be seen that, while the parameter values, as specified by Eq. 14, are identical for all neurons, the firing rate dynamics captured by the four categories, are highly diverse (as in a natural language, the same “words”, represented here by circuit polarity, or alternatively, by circuit firing modes, may belong to different categories).

Fig. 5 Firing rate simulation of the 2-neuron, 7-circuit polarity category depicted in column (a) of Fig. 4. In the first row, the two neurons are symmetrically connected, and, consequently, their firing rate modes are identical. In the second row, the first neuron is independently bursting, while the second is silent. In the third row, the second neuron is independently bursting, while the first is silent. In the fourth row, both neurons are silent. In the fifth and the sixth rows, while both neurons are active, their inter-connections are asymmetric, and, consequently, their firing rate modes are different. In the seventh row, the two neurons are mutually segregated by inter-neuron synapses, but, as their parameters are identical, their independent bursting firing rate modes are identical

“Working memory” and “magical numbers”

As cortical information appears to be manifested by neural circuit polarity and its consequential firing rate modes, the memory capacity of categories of small circuits, as the ones analyzed in the previous sections, is of interest. Employing experimental behavior data, it has been suggested that human capacity for information processing is limited by “the magical number seven, plus or minus two” (Miller 1956). Pertaining to “working memory” (Pribram et al. 1960), or, metaphorically, “blackboard memory” (Colman 2008), and later supported by a winnerless competition dynamical model (Bick and Rabinovich 2009), this limit has been associated with “one dimensional” objects (such as musical tunes, electrical skin stimulation, or visual dot location), while noting that “higher dimensional” objects (such as human faces) would require higher information processing capacities (Miller 1956). As we have noted in the present work, dimensionality of information items may be associated with prime factorization of composite polarity code-sizes. Specifically, in contrast to the single

Fig. 6 Firing rate simulation of the 2-neuron, 7-circuit polarity category depicted in column (b) of Fig. 4. In the first row, as the self-synapses of the two neurons are at different polarity states, their firing rate modes are different. In the second row, the first neuron is independently firing, while the second is silent. In the third row, the second neuron is independently firing, while the first neuron is silent. In the fourth row, both neurons have silent membranes. In the fifth and the sixth rows, differences between interneuron connections and self-synapses are compensated by cross-feedback, and consequently, the firing rate modes are identical. In the seventh row, the two neurons are mutually segregated, but, since their self-synapses are at different states, their firing rate modes are different

primal polarity code sizes corresponding to circuits of 1–4 neurons, which may be characterized as having a single dimension, the three different primal polarity category sizes obtained by factorization of *sphenic* (Lehmer 1936) polarity code sizes corresponding to circuits of 5, 6 and 7 neurons may be characterized as representing three different dimensions. Another proposition has suggested “the magical number four” (or, more specifically, “between three and five”, Cowan 2001) instead of “the magical number seven” (Miller 1956). We note that, as seen in Table 2, the number 7 appears as the polarity category size for a circuit of 2 neurons, while the number 4 appears as the polarity code size for a single neuron. This may suggest that the two numbers, 7 and 4, have been experimentally measured in two different contexts, one of a single category of items, represented by 2-neuron circuits with axonal discharge self-feedback, and the other of two different categories of items, represented by 1-neuron circuits with synaptic self-feedback. A division of memory into separate domains of small and large numbers of information items, as suggested by the large spread of polarity category and code sizes represented by Table 2, has also been suggested

Fig. 7 Firing rate simulation of the 2-neuron, 7-circuit polarity category depicted in column (c) of Fig. 4. In the first row, the difference between the polarity states of the two self-synapses yields different firing rate modes. In the second row, the first neuron is independently firing, while the second is silent. In the third row, the second neuron is independently firing, while the first neuron is silent. In the fourth row, both neurons have silent membranes. In the fifth and the sixth rows, differences between cross-feedback compensation of the two neurons yield different firing rate modes. In the seventh row, the two neurons are mutually segregated, but, since their self-synapses are at different states, their firing rate modes are different

on experimental grounds (Cowan 1995). Indeed, outstanding processing abilities of many information items have been experimentally noted (Chase and Ericsson 1982; Yaro and Ward 2007; Neumann 2010).

A question of interest is whether there is a mathematical basis to “magical numbers” as memory capacities. A widely recognized concept of memory in the context of binary neuronal states is the Hebbian learning paradigm (Hebb 1949), which has been formalized as follows (McCulloch and Pitts 1943; Hopfield 1982). Consider a neural circuit of n neurons, whose membrane and synapse polarity states, $\omega_j(i) \in (0, 1)$, $j = 1, \dots, n$ at discrete times, $i = 1, \dots, M$, take the values 0 or 1 with equal probabilities. Storage of polarity state values is performed according to the rule

$$\omega_{k,j} = \sum_i^M \omega_k^{(i)} \omega_j^{(i)} \quad (15)$$

Retrieval is performed by the rule

$$x_k = \begin{cases} 0, & \text{if } u_k \leq t \\ 1, & \text{if } u_k > t \end{cases} \quad (16)$$

where t is a threshold and

Fig. 8 Firing rate simulation of the 2-neuron, 7-circuit polarity category depicted in column (d) of Fig. 4. In the first row, the identical polarity states of the two self-synapses, and the identical polarity states of the two cross-neuron synapses yield identical firing rate modes for the two neurons. In the second row, the first neuron is independently firing, while the second has a silent membrane. In the third row, the second neuron is independently firing, while the first neuron has a silent membrane. In the fourth row, both neurons have silent membranes. In the fifth and the sixth rows, differences between cross-feedback compensation of the two neurons yield different firing rate modes. In the seventh row, the two neurons are mutually segregated by silent interneuron synapses, and, having both their self-synapses silent, fire in identical firing rate modes

$$u_k = \sum_{j=1}^n \omega_{kj} z_j \quad (17)$$

is the input to the k 'th neuron, where z_j , $j = 1, \dots, n$ are the components of a probe.

The memory capacity of binary (0,1) vectors of size n by networks of the type Eqs. 15–17 has been shown to be about $0.14n$ (Amit et al. 1987). We note that, from a mathematical viewpoint, n may represent the number of circuit neurons, in one context, and the number of circuit polarity gates, in another. For polarity vectors of size 7, associated, as shown in the present work, with 2-neron circuits, this result would imply a Hebbian memory capacity, by Eqs. 15–17, of approximately one polarity vector per circuit ($0.14 \times 7 = 0.98$). A “working memory” consisting of 2-neuron circuits would allow for a maximum of 7 circuits having different polarity states, in each of the categories depicted in Fig. 4. With each of these circuits storing one polarity state vector, this would establish a neural embodiment of “the magical number 7” as the category memory capacity.

Discussion

A neural circuit polarity code is defined by the complete set of circuits generated by permutations of polarity states of the circuit neurons' membranes and synapses. For a given number of circuit neurons, a primal circuit polarity code size implies that the code is indivisible, constituting a circuit polarity category. The present paper has shown that when the circuit polarity code size is not primal, it can be factorized into primal-size subcodes, representing different categories, which, in turn, produce different firing-rate modes. Fully connected circuits of 1, 2, 3 and 4 neurons produce circuit polarity codes of primal sizes 2, 7, 71 and 4111, respectively. On the other hand, circuits of 5, 6 or 7 neurons produce circuit polarity codes of composite sizes. Such codes can be computationally transformed into primal size polarity categories by prime factorization of their polarity code sizes. The high dominance of the first term on the right-hand-side of Eq. 3 ($2^{n(n-1)}$) implies that such prime factorization is practically impossible by standard computational techniques for circuits of more than 7 neurons. It is conceivable that nature would have its way of producing primal-size polarity categories for circuits of more than 7 neurons. Yet, even without such capabilities, relatively large cortical areas may be aroused by smaller circuits interacting in a feedforward fashion.

The effect of neuronal self-feedback on primal polarity code size is particularly interesting in the context of a long-standing debate concerning the nature of such feedback. While, employing neurophysiological and molecular considerations, the synaptically mediated self-feedback paradigm (Groves et al. 1975) has been presented as an alternative to the axonal discharge self-feedback paradigm (Carlsson and Lindquist 1963; Smith and Jahr 2002), we have shown in this work that the first paradigm contains the second. Specifically, while the axonal discharge self-feedback paradigm defines a single, primal-size, circuit polarity category for certain fully connected circuit sizes (1–4), the synaptic self-feedback paradigm defines the entire range of such categories produced by permutation of self-synaptic polarity states. Consequently, the number of categories produced by the synaptically mediated self-feedback paradigm grows exponentially in the number of circuit neurons with respect to that produced by the axonal discharge self-feedback paradigm.

“Magical numbers”, supported by psychophysical tests of “absolute judgement” (Miller 1956), have been suggested as limit capacities for “working memory” (Pribram et al. 1960). While such numbers were not directly related to neurophysiological experiments, we have suggested that their small values (3–9 according to various publications) are resembled by the small circuit sizes suggested in the

present study as the “alphabets”, “words” or “categories”, of cortical information. We have also suggested that the level of prime factorization of circuit sizes constitutes a certain notion of informational dimension. The possible neurophysiological basis for such correspondence is proposed for future research.

Finally, we note that the practical advantage of primality may be explained by the ability of different prime numbers to generate large numbers of different combinations without repetition. This property has been characterized in purely mathematical contexts (Furstenberg 1955) and further in the geometric contexts of polygon construction and partition (Křížek et al. 2001). Its applicability in digital computation has been noted in the contexts of hash table generation (Cormen et al. 2001), error detection (Kirtland 2001) and pseudo-random number generation (Matsumoto and Nishimura 1998). Prime numbers have been shown to play fundamental roles in quantum physics (Peterson 1999) and in quantum computation (Bengtsson and Życzkowski 2017) as well as the natural survival game of predator and prey (Williams and Simon 1995), literature (Ribbenboim 2017) and music (du Sautoy 2003). Yet, it appears that the relevance of prime numbers in cortical contexts has not been noted before.

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