Computer simulations of synchrony and oscillations evoked by two coherent inputs

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Abstract Coherent oscillations have been reported in multiple cortical areas. This study examines the characteristics of output spikes through computer simulations when the neural network model receives periodic/asperiodic spatiotemporal spikes with modulated/constant populational activity from two pathways. Synchronous oscillations which have the same period as the input are observed in response to periodic input patterns regardless of populational activity. The results confirm that the output frequency of synchrony is essentially determined by the period of the repeated input patterns. On the other hand, weak periodic outputs are observed when asperiodic spikes are input with modulated populational activity. In this case, higher firing rates are necessary to input for higher frequency oscillations. The spike-timing-dependent plasticity suppresses the spikes which do not contribute to the synchrony for periodic inputs. This effect corresponds to the experimental reports that learning sharpens the synchrony in the motor cortex. These results suggest that spatiotemporal spike patterns should be entrained on modulated populational activity to transmit oscillatory information effectively in the convergent pathway.

Keywords Oscillation · Autocorrelation · Spike-timing dependent synaptic plasticity · Poisson trains · Neural network model

Introduction

Coherent oscillations have been reported in the motor related areas (Ohara et al. 2001; Lee 2003, 2004; Hatsopoulos et al.

1998; Grammont and Riehle 2003; Kilavik et al. 2009) as well as the other cortical areas (Roelfsema et al. 1997; Rodriguez et al. 2004). For example, 20 to 30 Hz oscillations related to an action have been observed in the premotor cortical neurons (Lebedev and Wise 2000). In addition, γ oscillations related to movement have been observed in the motor cortex recently (Chyne et al. 2008). γ oscillations are thought to be a fundamental process in cortical computation (Fries 2009). Precise synchronization among cortical areas suggest information processing such as visuomotor integration (Roelfsema et al. 1997).

On the other hand, it has been known that the SMA (supplementary motor area) has projections to the primary motor area and neurons in SMA and pre-SMA are activated during the preparatory period of action (Tanji and Kurata 1985; Kurata and Tanji 1985; Tanji and Shima 1994; Sakai et al. 1996; Cunningham et al. 2002; Isoda and Hikosaka 2007). Actually, oscillatory activity in the γ frequency synchronized immediately before and after the onset of movement in the SMA (Lee 2003). These results suggest the possibility that SMA neurons play a role in generation of synchronous spikes that trigger the motor cortical spikes with higher firing rates. If it is true, synchronous spikes with low frequent firing rates may be transformed into higher frequent spikes somewhere in the premotor areas including SMA and pre-SMA and the motor cortex.

Anatomically, the premotor areas including SMA and pre-SMA receive reciprocal projections from the parietal cortices through superior longitudinal fasciculus, and the targets of projection are slightly different depending on the area in the parietal cortices (Rizzolatti et al. 1998; Andersen and Buneo 2002). For example, while superior parietal lobule have reciprocal links with SMA and dorsal premotor region, caudal part of inferior parietal lobule has a major link to the prefrontal cortex (Wise et al. 1997; Petrides and

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Pandya 2002). The former pathway is thought to concern visuo-motor information and the latter pathway is to concern the perception and attention. On the other hand, some cortical areas receive projections from the dorsolateral prefrontal and posterior parietal cortices, which include cingulate cortices, superior temporal sulcus, and the premotor cortices such as SMA and pre-SMA (Selemon and Goldman-Rakic 1988; Lu et al. 1994). Among these complicated pathways, we can suppose at least two distinct pathways between the parietal cortex and the premotor cortex: one is from the parietal to the prefrontal cortices and the other is from the parietal to the premotor cortices. As shown above, the former mainly concerns higher information processing such as attention, and the latter likely concerns visual information such as position and characteristics of an object (Petrides and Pandya 2002, 2007).

These facts suggest that the interactions between parietal and prefrontal cortices have multiple channels, at least two channels of attention or inattention and characteristic information of an attended object. Thus we think that the information of attended target is shared between the parietal and prefrontal areas through parieto-frontal reciprocal connections. Once the target is locked on, this signal of attention is sent to both premotor and parietal areas. We assume that this state correlates with oscillations between these areas. At the same time, parieto-premotor interactions mainly concerned by the superior parietal cortex provide the premotor cortex with characteristic information of the target. As a result, oscillations and synchronies may occur in the premotor areas through multiple pathways from various areas such as dorsal prefrontal cortex and parietal cortices.

Assuming the two oscillating pathways to the premotor cortex (we call these pathways “top-down” and “bottom-up”), we can think that oscillations and synchronies occur by means of the two series of inputs with oscillations (Riehle et al. 1997; Vaadia et al. 1995). The purpose of this study is to examine the characteristics of output spike patterns when two series (top-down and bottom-up) of periodic spatiotemporal patterns are input to the neural network model in computer simulations.

Methods

This section explains the details of the neural network model. First, the model neuron which composes the neural network is clarified, then the network structure and the synaptic plasticity are described.

At macroscopic level, the cortex consists of six layers and there exist interactions between the layers. In this study, to focus on the activities of the neurons, where two coherent oscillations are input to convergently, our simplified neural model assumed to be in the same column that

receives signals from different cortical areas. In our model, one unit of the model synapse represents an average over hundreds of synapses for simplicity. Thus the standard deviation of synaptic weight will decrease to 10^{-1} . Although each synaptic weight is unreliable device (Freche et al. 2011), we approximate each unit weight as a mean value. Thus, the present study focuses on, so to speak, mesoscopic phenomena of oscillatory neuronal activities (Foster et al. 2008; Guo 2011; Schütt et al. 2012).

Model neurons

Assuming that each neuron is a leaky integrate-and-fire model, the internal potential $V_i(t)$ of i neuron follows the differential equation as follows:

$$\tau \frac{dV_i(t)}{dt} = V_{rest} - V_i(t) + \sum_j w_{ij} f(V_j(t)) (E_0 - V_i(t)) + I, \quad (1)$$

where $\tau = 20$ is a time constant, V_{rest} is a resting potential, w_{ij} is the synaptic efficacy from j to i neuron, $f(x)$ is an output function which corresponds to 1 if x is greater than the threshold θ and 0 otherwise, I is an input to this neuron, and E_0 is either of excitatory (E_{ex}) or inhibitory (E_{inh}) potential which depends on the j neuron is an excitatory (80 %) or inhibitory (20 %) neuron. When $V_i(t)$ reaches the threshold θ , $V_i(t)$ is reset to V_{rest} , and the third term of right side of Eq. (1) is also reset to zero. The absolute refractory period is set to be 1 ms. The number of neurons is 200. The parameter values are as follows: $E_{ex} = 0$, $E_{inh} = -100$, $V_{rest} = -65.0$, and $\theta = -60.0$.

Network model

The probability of a model neuron receiving a synaptic projection from another neuron is 20 %. There is no recurrent connection for itself. Thus the synaptic connections between neurons are not fully connected but sparse (20 %). This is because the biological brain has such sparse connections (Braitenberg and Schuz 1991). Eighty percent neurons are excitatory and the rest are inhibitory to avoid bursting by recurrent connections as in the real cortices. The amplitude of each initial synaptic weight is randomly chosen from 0.5 to 1.0. The inputs to each neuron are bottom-up (sensory) and top-down signals from outside the focused network (we call “external inputs”) as well as synaptic inputs from within the focused network. The external input I in Eq. (1) denotes the sum of the bottom-up and top-down inputs.

This model receives two series of external inputs to each neuron, thus each series is a spatiotemporal pattern. One series is supposed to be bottom-up signals such as sensory signals of a target object, and the other series is supposed to

be the top-down signals such as information about sensory-motor processing. In this study, each of the input signals assumes to oscillate in the same frequency and in the same manner if an object is attended and/or the object is recognized, respectively. Thus the spatiotemporal patterns of the two external inputs are different, but the features (i.e. Poisson or Gaussian-modulated trains and repetitive period) are the same and we do not distinguish them. We set the strength of external inputs to a constant value so that alternative inputs of the top-down or sensory signal provided to the interconnected network cannot solely evoke the sufficient response for synchrony.

Spike-timing dependent synaptic plasticity

If sensory and top-down signals are input to the interconnected neural network model with spike-timing dependent synaptic plasticity (STDP) (Markram et al. 1996; Bi and Poo 1999), the network learns the transformation from the input spatiotemporal pattern into a synchronous spike (Kitano and Fukai 2004; Hosaka et al. 2008). As the previous studies, STDP is assumed to be applied only to the connections between excitatory neurons. The relation between pre- and postsynaptic spike timings and change of synaptic weights shows an exponential curve. We adopted the typical algorithm shown by Song et al. (2000) as follows: Every time the postsynaptic neuron fires an action potential, the value $M_i(t)$ of neuron i is decremented by an amount A^- , and every time synapse a receives an action potential, $P_a(t)$ is incremented by an amount A^+ . Thus $M_i(t) \leq 0$ and $0 \leq P_a(t)$. $M_i(t)$ and $P_a(t)$ decays exponentially as the time proceeds. The time constant of exponential decay is 40 ms. When a spike reaches the synapse of neuron i , $wM_i(t)$ is added to the synaptic weight w . If $M_i(t)$ is negative, this addition implies synaptic depression. On the other hand, when a neuron fires, $wP_a(t)$ is added to the synaptic weight w of every synapse a of the neuron. If $P_a(t)$ is positive, this implies synaptic potentiation. The parameter values are as follows: $A^- = 0.1$ and $A^+ = 0.1$.

Results of computer simulations

Two factors of input trains: populational activity and spike patterns

In generation of oscillatory input patterns, we considered two independent factors as follows: (1) populational activity: sinusously modulated or constant, and (2) spike patterns: repeated spatiotemporal pattern or aperiodic. Thus we assume four input types, that are periodic/aperiodic pattern with modulated/constant populational activity. We suppose that some important information is represented by the

spatiotemporal input pattern. Since the spatial pattern means which neuron to be input, the temporal pattern is the key to determine the properties of the spatiotemporal pattern.

Concerning the first factor, the populational activity, it has been reported that cell assemblies synchronously occur in accordance with LFP sinusoidal oscillations in the cortex (Harris et al. 2003; Shu et al. 2003). To adopt this activity as an input, we assume that the population activity is sinusoidally modulated. On the other hand, spontaneous EEG on awakening shows irregular, higher frequency, and low-amplitude waves (Steriade et al. 1996; Destexhe and Contreras 2006). In this case, the population activity can be regarded as almost constant. Concretely, we assume two ways of generating spike patterns: “Gaussian-modulated” and “Poisson trains” for modulated/constant populational activity, respectively. In the Poisson trains, the interstimulus interval (ISI) of each train input to each neuron follows an exponential distribution with a constant average. The interspike interval is assumed to follow an exponential distribution (Poisson point process) because such irregular spikes are observed in the cortex (Softky and Koch 1993; Bair et al. 1994). The spatiotemporal pattern is generated by independent Poisson trains with a common mean ISI (50 ms in the simulations unless otherwise stated). The reciprocal of mean ISI denotes the mean input frequency. In the case of Gaussian-modulated input trains, the probability of occurrence of input spikes follows a Gaussian density function. While the probability density of input spikes is almost plain in Poisson trains, that is biased in Gaussian-modulated trains.

Second, about spike patterns, it has been reported that a specific spatiotemporal pattern is repeatedly observed in the cortical neurons (Ikegaya et al. 2004; Cossart et al. 2003). We assume that a spatiotemporal spike pattern which occurs repeatedly should contribute to oscillatory phenomena as observed in LFP. Thus, we consider two more cases that the spatiotemporal pattern for input consists of repeated patterns of a specific spatiotemporal pattern (periodic) or not (aperiodic). In the repeated input, a spatiotemporal pattern during a constant period is repeatedly applied as an external input. Thus, there are two cases for each of modulated/constant populational activity: one consists of exactly repeated patterns and the other of aperiodic patterns. Let the duration of the repeatedly input pattern is T in the former case. Figure 1 shows an example of the periodic pattern with constant populational activity. These patterns are independent Poisson trains as shown above. Note that the specific spatiotemporal pattern between $t = 100$ and $t = 150$ is repeated six times from $t = 100$ to $t = 400$. Figure 1 (bottom) shows almost 20 spikes/s, which corresponds to the reciprocal of the mean ISI.

In the case of modulated populational activity, in each period of the modulation T , we define a shifted Gaussian

Fig. 1 An example of periodic pattern with constant populational activity. Note that the specific spatiotemporal pattern between $t = 100$ and $t = 150$ ($T = 50$ ms) is repeated from $t = 100$ to $t = 400$. The *top figure* shows the raster pattern of the inputs. The *bottom one* shows the mean input spikes per second over all 200 neurons within a sliding window of 10 ms at each time

Fig. 2 An example of aperiodic pattern with modulated populational activity (the modulation period is $T = 50$ ms). Note that the specific spatiotemporal pattern between $t = 100$ and $t = 150$ is NOT repeated from $t = 100$ to $t = 400$. The *top figure* shows the raster pattern of the inputs. The *bottom one* shows the mean input spikes per second over all 200 neurons within a sliding window of 10 ms at each time

density function which has a peak at $t = Tk + \frac{T}{2}$ ($k \geq 0$ is an integer) and its variance is $T/4$. Following this density function, we determined the time when each spike will be input. To deal with the input rate for each neuron independently of the period T , the total number of inputs per neuron were determined from the total duration divided by the assumed ISI. Since this divided value is not always an integer, an integer as the number of inputs is probabilistically selected within the specific range for each neuron in the simulation procedures. As a result, since the ISI is set to 50 ms, mean input spike rates for Poisson and Gaussian-modulated spikes are almost the same as 20 Hz. If the period of modulation is $T = 50$ ms, the frequency of Gaussian-modulation is also 20 Hz. Figure 2 shows an example of aperiodic pattern with modulated populational activity (the modulation period is $T = 50$ ms). Note that the population-averaged input (Fig. 2 bottom) shows Gaussian density on the contrary to Poisson trains (Fig. 1 bottom). In the simulations, we would like to change T with fixed mean ISI.

When two inputs have a constant populational activity

Different Poisson trains generated from different random seeds with the same mean ISI and the same feature (periodic or aperiodic) are input to each model neuron as top-down

and bottom-up signals. Without STDP, synchronous spikes sometimes occur but not periodically as Fig. 3 (top) shows a typical example of raster plots when two independent inputs are periodic Poisson trains (one of the two spatiotemporal patterns is the same as shown in Fig. 1). Figure 3 (bottom) shows the populational activity, that means spike rates per second averaged over 200 neurons within a sliding windows of 10 ms at each time. Figure 4 shows a case with STDP in response to the same input trains as in Fig. 3. While Fig. 3 (bottom) shows aperiodic populational activities with some bursts, Fig. 4 (bottom) shows relatively periodical wave. In other words, periodic synchronies were much observed in the neural network model with STDP, while aperiodic spike patterns were remarkably observed in the model without STDP. This result is correspondent with the results of previous numerical studies (Kitano and Fukai 2004; Hosaka et al. 2008). In the previous study, the transformation function of STDP from a spatiotemporal pattern into a synchrony has been examined and analyzed using computer simulations (Hosaka et al. 2008). According to this literature, the connections correspondent with cause-and-effect spike relations in the spatiotemporal structure of the input pattern are strengthened and the others are weakened by STDP. This forces the flows of spikes to trigger a synchronous spike like an avalanche. Once a synchrony occurs, excited inhibitory neurons suppress other neurons for a while in addition to refractory effect. These effects spend

Fig. 3 The outputs of the network model without STDP (synaptic plasticity) in response to the periodic patterns with constant populational activity. The length of the period is 50 ms (from $t = 100$ to $t = 400$). The output raster plots (top) and populational firing rates (bottom)

Fig. 4 The outputs of the network model with STDP in response to the periodic patterns with constant populational activity. The length of the period is 50 ms (from $t = 100$ to $t = 400$). The output raster plots (top) and populational firing rates (bottom)

some time before the next wave is elicited, then the synchrony easily occurs periodically. In this case, since there is no sinusoidal temporal modulation in the input populational

Fig. 5 The autocorrelation of population-averaged spikes

activity, periodic activity seldom occurs if the input spike pattern is aperiodic.

To focus on the spikes which contributes to synchrony, we calculate the autocorrelation (Fig. 5) of the raster plots shown in Fig. 4 (top). Here, the autocorrelation at time t is defined by counting coincident spikes within ± 1 ms precision when the trains in the sliding window are temporally shifted for Δt around the time t . The temporal width of the window is set to be 160 ms, then the focused range is from $t - 80$ to $t + 79$ ms. The counts are normalized by the total spike number in the sliding window. To highlight the changes in the area of $\Delta t \neq 0$, those data at $\Delta t = 0$ are omitted from all of the autocorrelation figures shown in this paper. Figure 5 clearly shows that the spatiotemporal output in Fig. 4 includes the oscillatory pattern whose period is $T = 50$ ms.

When we change the value of T , duration of the repeated pattern, we observed that the period of synchronies of output spikes change depending on T . The autocorrelations at $t = 250$ ms when $T = 20, 40$, and 50 ms respectively, averaged over 100 times for different input patterns and initial synaptic weights generated from different random seeds, are shown in Fig. 6. This result shows that the temporal relationship commonly input from two sources is strengthened and maintained, whether STDP works or not. In addition, Fig. 6 suggests that STDP contributes to suppress noisy signals unrelated to the periodic spikes. This is because STDP weakens the synaptic weights that do not contribute to the synchrony. When aperiodic Poisson trains (i.e. standard Poisson trains) are input, we observe no remarkable peak in the autocorrelation (figures are shown later in Figs. 9, 10). In this case, STDP does not seem to work as a noise suppressor at all.

When two inputs have a modulated populational activity

Similarly, periodic input patterns with modulated populational activity through two pathways tend to make synchronous spikes even without STDP (Fig. 7). As is observed in the case

Fig. 6 Mean autocorrelations of output spikes (*top*: without STDP, *bottom*: with STDP) in response to the periodic patterns with constant populational activity. **a** Without STDP, **b** with STDP

of constant populational activity, the synchrony becomes sharper than that before STDP is introduced. Consequently, Gaussian-modulated inputs with coherent phase tends to evoke synchrony even without STDP, whereas STDP seems to contribute to noiseless synchrony. When we change the value of T , duration of the unit of Gaussian-modulation of input trains, we observed that the period of synchronies of output spikes change depending on T as shown in non-modulated populational activity. When $T = 20, 40$, and 50 ms, the autocorrelations at $t = 250$ ms averaged over 100 times for different input patterns and initial synaptic weights are shown in Fig. 8. This result shows that the periodicity of Gaussian-modulation is maintained regardless of synaptic plasticity. Since the input populational activity is modulated by the Gaussian function, the neurons tend to fire in the phase of increased activity but they do not in that of decreased activity because of the integral property of neuron. This makes the periodical firings clearer than the case of Poisson trains (Figs. 6, 7, 8). This means that the periodic input pattern with modulated populational activity

Fig. 7 The outputs of the network model with and without STDP in response to the Gaussian-modulated trains with periodicity of 50 ms (from $t = 100$ to $t = 400$). **a** Without STDP, **b** with STDP

makes output periodicity more effectively among four input types. STDP contributes to suppression of noisy signals which are unrelated to the periodic spikes in this case, too.

When aperiodic Gaussian-modulated trains (an example is shown in Fig. 2) are input, the results differ from those of aperiodic Poisson inputs (constant populational activity). Figure 9 shows mean autocorrelations of output spikes with and without STDP. The values when the inputs are aperiodic

Fig. 8 Mean autocorrelations of output spikes (*top*: without STDP, *bottom*: with STDP) to the periodic input patterns with modulated populational activity. **a** Without STDP, **b** with STDP

Poisson trains are also plotted for comparison. The aperiodic Poisson trains indicate naive Poisson trains without periodicity. When the period of Gaussian modulation $T = 40$ ms without STDP, there are two peaks of 0.094 at $\Delta t = 4$ and 0.081 at $\Delta t = 40$. When $T = 50$ ms without STDP, two peaks are 0.080 at $\Delta t = 4$ and 0.071 at $\Delta t = 52$. Similarly, with STDP, the peaks are 0.041 at $\Delta t = 4$ and 0.042 at $\Delta t = 40$ when $T = 40$ ms, and 0.032 at $\Delta t = 4$ and 0.042 at $\Delta t = 50$ when $T = 50$ ms. The peaks close to $\Delta t = 0$ are due to bursting spikes. In the cases of $T = 20$ ms and Poisson trains, peaks are not clear in Fig. 9. These data show that the autocorrelations by aperiodic inputs are much weaker than those by periodic ones. Residual little periodicity in Fig. 9 is due to the modulation of populational activity.

When mean ISI decreases to 40 ms, the autocorrelation of $T = 20$ ms becomes clearer (Fig. 10). This means that the mean firing rate of each input train needs as much as the expected output frequency in order to synchronize with modulated populational activity using aperiodic spike patterns.

Fig. 9 Mean autocorrelations of output spikes (*top*: without STDP, *bottom*: with STDP) to the aperiodic input patterns with modulated/constant populational activity. The mean ISI is 50 ms. **a** Without STDP, **b** with STDP

Even if aperiodic spikes are input, almost synchronous spikes are input to the neurons because of the periodic populational modulation. However, this single effect is not satisfactory for periodic fires because the input neurons are selected stochastically. On the other hand, a specific group of neurons whose input synaptic weights are relatively larger tend to fire more frequently through interactions within the neural network (Araki and Aihara 2001). Therefore, this effect will increase the autocorrelation a little. In the case of aperiodic inputs, introducing STDP plainly decreases the autocorrelation because the orders of pre- and post-synaptic spikes are almost random.

Discussion

First, let us summarize the results. We clarified the effects of two input factors, i.e. periodic/aperiodic spatiotemporal

Fig. 10 Mean autocorrelations of output spikes with STDP to the aperiodic input patterns with modulated/constant populational activity. **a** Mean ISI is 40 ms, **b** mean ISI is 25 ms

spikes and modulated/constant populational activity on the periodicity of output spikes, using a simple neural network model. Synchronous oscillations which have the same period as the inputs are observed when the two patterns are input, except when aperiodic spikes with constant populational activity are input. When specific spatiotemporal spikes are periodically input, mean input frequency into each neuron does not need as high as the output frequency even if the populational activity is constant. This is because the period of output oscillation is not decided by the input frequency, but by the period of the input spatiotemporal pattern. In contrast, in the case of aperiodic inputs with modulated populational activity, higher frequent input spikes are needed for higher frequency oscillations in the outputs. For aperiodic input patterns, STDP neutrally suppresses all spikes, because the temporal timings of spikes between pre- and post-synaptic neurons are irregular. In contrast, for periodic patterns, STDP can suppress temporarily generated noisy spikes that have less temporal relations. This result is correspondent with the physiological

experiment reports that the synchrony in the motor cortex becomes stronger and more localized in time with improvement of behavioral performance as the learning proceeds (Kilavik et al. 2009).

Taken together, periodic spatiotemporal patterns will be better than populational modulation as a method of information transmission in oscillatory waves. Since the populational modulation is stable at lower frequency and robust for aperiodic noises, it might be fit for ready state like an idling (Weigenand et al. 2012). Actually, in the simulations, the input spikes with both properties, i.e. periodic spikes and modulated populational activity, are the best for strong and noiseless autocorrelation. Therefore, the results suggest a good way to transmit oscillatory information in the convergent pathway as follows: spatiotemporal spike patterns should be entrained on modulated populational activity. Then it must be natural that both of modulated waves and spatiotemporal spikes are observed in the brain. The direct evidence of spatiotemporal patterns are few, but a transient synchrony such as “unitary event” has been reported (Kilavik et al. 2009; Grammont and Riehle 2003). Some transient synchronies organized by cell assemblies (Singer 1999, 2009) may contribute to a transient spatiotemporal pattern. These transient or short-term synchronies may be observed in longer time scale as higher frequency wave such as a β or γ wave.

According to the previous numerical study, it is known that a synchronous spike occurs only if the learned spatiotemporal pattern is input after synaptic learning (Hosaka et al. 2008). The synchronous signal can activate the primary motor cortex, which will induce the movement. If the model learns the transformation from a spatiotemporal to a synchronous pattern, both of sensory and top-down signals are necessary to synchronous spikes. Concretely, when the sensory signals are input without the top-down signal or the top-down signal is on without the sensory signal, synchronous spikes seldom occur. Therefore, when the top-down signal is received, we can consider that this circuit waiting for the specific sensory input is in the ready state to trigger the movement.

The generated synchrony (or oscillations) may contribute to the functions such as making links between areas (Fries 2009), control the flow of information (Lee 2004), or integration of sensory and other information (Roelfsema et al. 1997). The results suggest that each frequency band such as α , β , γ differs in the generation mechanism and the role of information processing in the brain.

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