Neuronal Oscillations and Synchronized Activity in the Central Nervous System: Functional Aspects

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Abstract

Quite a number of experimental findings are consistent with the idea that gamma wave oscillations and synchronized activity in the central nervous system are the basis of higher functions of the nervous system (cell assembly theory). However, there is as yet no direct proof that this theory is correct. Here an alternative hypothesis is presented, which provides a different interpretation of many of the observed phenomena. In this view, oscillations in the nervous system are the consequence of a mechanism for gain control that establishes an optimal compromise between the response time and the stability of the system.

Commentary on:	Lutzenberger, Werner and Preissl, Hubert and Pulvermueller, Friedemann and Pantev, Christo and Elbert, Thomas and Eulitz, Carsten (1994) Brain Rhythms, Cell Assemblies and Cognition: Evidence from the Processing of Words and Pseudowords, Psycoloquy: 5,#48 Brain Rhythms (1)
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1. In the target article (Pulvermueller et al., 1994), it is shown that meaningful words heard by an experimental subject elicited cortical responses in the region of 30 Hz that were significantly larger than when meaningless pseudowords were presented. This result is consistent with the concept of "Hebbian cell assembly theory" and was so interpreted by the authors. In itself, like a number of other published findings (Eckhorn, 1991; Singer, 1993; Singer and Gray, 1995), this result is of course not sufficient to establish the validity of the theory. In this situation it seems reasonable to look for some alternative

explanations. When alternatives are available, there is a chance that the different hypotheses will suggest different prognoses for different experimental paradigms, so that in the best case one or another of the hypotheses can be refuted. In the following, such an alternative to the concept of the Hebbian cell assembly theory will be formulated as an explanation of neuronal oscillations.

2. Oscillatory activity which can be recorded with large scale electrodes is a fundamental neural phenomenon (Adrian, 1937). This also means that synchronized activity of neurons is common, because otherwise their oscillatory activity -- if not in phase -- would cancel out. To consider only the vertebrate visual system, oscillations appear not only in the cortex but even in the retina (Przybyszewski et al., 1993) and, unexpectedly, in the lateral geniculate nucleus (Sillito et al., 1994). Because such peripheral structures are presumably not responsible for cognitive processing, here at least the functional significance of the oscillations is not a priori likely to be found in the context of the cell assembly theory, which is considered to be related to higher functions.

3. The hypothesis formulated below takes as a point of departure the following problem: In comparison with the components of computers, neurons have two substantial disadvantages as information-processing elements:

(i) Their dynamic range is limited. In the circa 100-ms time window relevant to perception, at most 100 different values can be encoded (5 or 6 bits). A cortical neuron is actually restricted to only about 4 different functional states (Barlow and Foeldiak, 1989). Because of this small dynamic range, the neurons must continually adjust their gain to the momentary input signals to ensure both that the output of each neuron is not overdriven by the input and that the neuron does not become so insensitive as not to respond to the input.

(ii) Nerve cells are relatively slow components; they usually cannot transmit frequencies higher than about 100 Hz as a parameter of the stimulus, for example, flicker rate of light flashes (although spikes can be discharged at higher frequencies). Evidently, then, it is important for their already poor temporal resolution not to be further degraded.

4. One way to alleviate both limitations efficiently is illustrated in Figure 1 below. Owing to the cable properties of dendrites, when synaptic potentials are induced, there is a limit to the speed with which they can change the membrane potential at the spike-generating locus. In the schematic circuit diagram, part (a) of Figure 1, the cable properties are simulated by a low-pass filter LP. D represents a delay, which is always present. k1 and k2 are amplification factors. Part (c) shows an example in which -- for the case of a stepwise input signal x (illustrated in part b) -- the output signal y rises gradually and reaches the threshold Th relatively late. A means of making the rise time shorter is to introduce a negative-feedback loop: the output signal y is multiplied by the gain k2 and subtracted from the input signal x (a). By increasing the overall gain k1 * k2, the rising phase can be made faster so that the the threshold is reached sooner (d). If k1 * k2 is further increased, the threshold is reached still sooner but oscillations appear in the response (e). Any greater increase of k1 * k2 makes the system unstable. In technical

systems designed to display an input value with minimal error, k1 * k2 would need merely to be raised by about the amount represented in (d), so that the response to a step input overshoots slightly but has no tendency to oscillate thereafter. The input x in the figure could represent, for example, activity of thalamic (LGN) cells, and y the activity of cortical neurons. Both are connected by a feedback loop (Sillito et al., 1994).

(a) x input (b) o o o o o o o o o o o o o o o o o o negative feedback o o o o o o o o o o o o o-o-o-o-o---------------------------- o o o o o o (c) o o o o L P o o - -Th- - - - - - - - -o- - o D o o o o o o o o o o o o o o o o o o k2 o o-o-o-o-o--------------------------- o o o o o o (d) o o o o o o o o o o o o o o o o o k1 o o - -Th- - - - -o- - - o o o o o o o o o o o o o o o o o o o o-o-o-o-o----------------------------- o (e) o y output o o o o o o o o - -Th- - -o- - o o o

o o-o-o-o-o----------------------------

FIGURE 1 --

5. In the nervous system there is the problem that the time constants of the nerve-cell membranes change -- for example, due to changes in the number of open channels -- so that the overall gain k1 * k2 must continually be adjusted according to the current situation, in order to avoid instability on the one hand while on the other preventing the system from responding too slowly. It is not a simple matter to arrive at a condition as shown in (d). But it is possible to maintain the state shown in (e) automatically, according to the principle of "gain control by feedback oscillations". This principle was first established for the optomotor control system of arthropods, and the way it operates was demonstrated by model calculations (Kirschfeld, 1991).

6. Characteristic properties of such a systems are as follows:

(i) The overall gain of the system rises spontaneously until, with the assistance of the noise constantly present in such a system, relatively high-frequency oscillations appear, for example, in the membrane potentials of nerve cells.

(ii) These oscillations are used as a signal to activate a mechanism that prevents the gain from increasing further. The result is that the system does not become unstable. [NOTE 1].

(iii) The system is therefore automatically kept in state (e), a compromise between high temporal resolution and stability.

(iv) It is important for the frequency of the oscillations to be high enough not to interfere with the signals passing from x to y. In the visual system, with a flicker fusion frequency of about 20 Hz, frequencies in the gamma-wave range (30-80 Hz) would not cause any disturbance.

7. A system like this, constantly on the brink of instability, has the following additional characteristics:

(i) A brief stimulus induces oscillations in principle like those in Figure 1, part (e). Because they are stimulus-induced, they can be extracted from the noise -- for example, in the EEG -- by stimulus-synchronized averaging techniques. Such oscillations have been demonstrated, for instance, at frequencies in the alpha-wave region for visually evoked potentials (Lansing and Barlow, 1972). Corresponding stimulus-induced oscillations can also be observed in the spike rates of cells of a nucleus (nBOR) in the accessory- optical system of pigeons (Wolf-Oberhollenzer and Kirschfeld, in prep.), and they can also be induced in the gamma-wave region in human cortex (Llinas and Ribary, 1992).

(ii) Even when no stimulus is presented, spontaneous oscillations ought often to occur, but because they reduce the gain their amplitude should in turn decrease; as a result, so-called "spindles" appear, for instance in the EEG. With averaging techniques, spontaneous oscillations can be extracted from the noise if the sweeps are triggered not by a stimulus but phase-synchronously. The frequency of these spontaneous oscillations would be expected to correspond to that of the stimulus-induced oscillations, because oscillation frequency is determined by the parameters of the feedback loop (delay, low-pass filter characteristics) and not by those of the input. That this is indeed the case has been shown both for alpha-waves (Lansing and Barlow, 1972) and for spontaneous and stimulus-induced oscillations of cells of the nBOR of the pigeon brain (Wolf-Oberhollenzer and Kirschfeld, in prep.).

(iii) It has been shown for gamma-waves that their amplitude increases as a subject becomes more attentive (Bouyer et al., 1987). According to the hypothesis proposed here, this response corresponds to a gain increase in the part of the CNS concerned with processing the signals originating in the object toward which the attention is directed [NOTE 2].

8. Now the functional consequences of the two hypotheses or theories will be compared. The "Hebbian cell assembly theory" will be termed Hypothesis H, and "gain control by feedback oscillations" will be called Hypothesis G.

(i) When a region of the CNS is in a state corresponding to Figure 1, part (c) or (d), thresholds for spike generation are exceeded, and according to Hypothesis G the system is therefore functional -- for instance, an object can be identified. However, the response would be slower than in state (e), in which the gain is higher; this represents the case in which attention is directed to the object. According to the assembly theory, on the other hand, an object would not even be identifiable unless the system is in state (e), because it is only then that the assembly of neurons is formed. The fact that oscillations are not always found, even when objects are identified, can be reconciled with Hypothesis G but less readily with Hypothesis H.

(ii) If synchronization and oscillations appear after presentation of a particular stimulus, Hypothesis H explains them in terms of the formation of an assembly associated with the presented object. The interpretation according to Hypothesis G is as follows. Assume that an object is identified and attracts attention to itself. To improve perception, the gain is raised, so that oscillations occur. The gain can remain high and the oscillations persist even after the object has vanished or changed, as long as attention is directed to the place where the object was. That is, Hypothesis G does not demand a precise temporal synchronization between perception of an object and the occurrence of oscillations.

(iii) One of the most interesting electrophysiological findings in this context is that even neurons widely separated from one another in the brain can synchronize their activity. According to Hypothesis G such synchronization occurs when the feedback loops are not limited to a single channel (as in Figure 1, part a) but extend to neighboring or more distant elements, in the sense of lateral backward inhibition (Kirschfeld, 1992). This finding does not allow either of the hypotheses to be refuted.

9. The Hebbian cell assembly theory would imply that after meaningful words have been heard, larger-amplitude oscillations in the gamma-wave region would appear in the EEG than in response to pseudowords. According to Hypothesis G, this finding is interpreted as follows: only meaningful words excite attention, and hence only they cause an increase in gain and in oscillation amplitude.

NOTE 1: A mechanism that could achieve this involves voltage- dependent, rapidly inactivating Ca channels (in cooperation with Ca-activated K+ channels): as the membrane potential oscillates, such channels are periodically opened at the frequency of the oscillation. Therefore more Ca can flow into the cell and more calcium-activated potassium channels will open. The latter reduce the membrane resistance, act as a shunt and thus reduce the gain.

NOTE 2: There are surely various mechanisms that could produce a local gain change. One might consist in a local negativity that lowers the thresholds of cortical cells. The probability that such cells will discharge is thereby increased, which amounts to a change in the gain (Birbaumer et al., 1990).

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Alternative Locations: UNSPECIFIED