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Neuron as time coherence discriminator

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Abstract. Neuronal excitability under stimuli with a complex time course is investigated on the basis of the numerical solution of the Hodgkin-Huxley equations. Each stimulus is composed of 100-1000 unitary excitatory postsynaptic potentials (uEPSP) that start randomly within a definite time window. Probability of initiating a spike [firing probability, $FP(W)$] as a function of the window width W is calculated by the Monte Carlo method. $FP(W)$ has a step-like shape: it becomes equal to 1 for small W and almost vanishes as W exceeds some value W_S. The role of long-lasting somatic inhibition is analysed. W_S depends on the inhibition potential, but the step-like shape of FP is preserved. It is concluded that the capability of multisynaptic stimulation to cause a spike can be expressed in terms of temporal coherence between the synaptic inputs. Namely, the spike is initiated if the temporal coherence between active inputs is above a definite threshold. The threshold value can be effectively regulated by varying the inhibition potential.

1 Introduction

Neuronal excitability under different stimuli is characterized by different criteria. If step-like and constant stimulations are considered, then threshold-type criteria with respect to voltage, charge or current apply (Noble and Stein 1966). Other criteria have been proposed for firing if a neuron is stimulated by single unitary excitatory postsynaptic potential (EPSP) (Kirkwood and Sears 1982; Fetz and Gustafsson 1983). These criteria express the capability of an EPSP to cause a spike in terms of the stimulus voltage and its time derivative.

At the same time, under natural conditions, the summation of many unitary EPSPs is necessary to initiate a spike (Coombs et al. 1955). The rate of synaptic stimulation into a single cell is estimated as 100 000 EPSPs/s (Abeles 1982). The minimal number of synchronous EPSPs needed to cause a spike in a pyramidal cell is estimated experimentally to be between 100 and 300 (Andersen et al. 1990). The figures must be increased if, firstly, the EPSPs are not perfectly synchronous and, secondly, the cell is inhibited.

In the case of multiple stimulation, the compound postsynaptic potential possesses the complicated time course that results from summation of the unitary EPSPs in the soma domain. In this case we may doubt the applicability of the voltage-threshold criterion, for the reason that in the excitable membrane the interaction between voltage-dependent inward and outward currents is temporally non-local. To be precise, the membrane voltage determines the rate constants rather than the conductances themselves. That is why the stimulus time course may play an essential role.

The purposes of this paper are as follows. First, we aim to examine the applicability of the voltage-threshold criterion for complex stimuli composed of three or more identical unitary EPSPs. Second, we study the influence of the relative timing within the compound postsynaptic potential on the ability of the stimulus to cause a spike. Finally, we intend to formulate the role of inhibition in the context of timing.

It is worth noting that giving a description of an actual neuron is not our purpose here. The present study is carried out within the Hodgkin and Huxley (1952) model. This model incorporates dynamical properties which are generic for neurons: non-linearities, and non-locality in time of the interaction between different currents. The paper focuses on the following question: How does the degree of temporal coherence of the compound stimulus affect the ability of the stimulus to fire a neuron possessing the above generic properties?

For stimuli composed of many weak EPSPs it is possible to formulate the firing criterion in a threshold-type manner. Namely, the stimulus is successful if it is composed of EPSPs starting within a definite time window, and unsuccessful if the starting times are distributed over a wider window. The successful window width can be varied from zero to several tens of milliseconds by varying the hyperpolarization voltage.

2 Methods

2.1 Parametric approach for complex stimuli

The theory of dynamical systems tells us that several coupled non-linear equations have normally a rather complicated dynamical behaviour. There

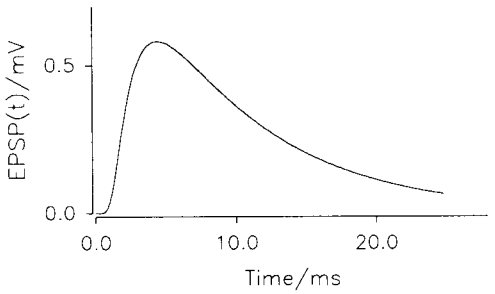

Fig. 1. The unitary excitatory postsynaptic potential (EPSP) time course, $EPSP(t)$, used for numerical simulations with input number NP = 100. For NP = 1000 and three EPSPs the values were scaled (see text and Fig. 2 legend)

are some examples of such behaviour for equations of the Hodgkin-Huxley type (e.g. Canavier et al. 1993). Therefore, the existence of a simple universal criterion for estimating the capability of a complex stimulus to cause a spike is unlikely. In the general case, a unique possibility for predicting the neuronal response to a stimulus with a complicated time course is to solve the Hodgkin-Huxley type equations directly and analyse whether a spike does appear.

On the other hand, some sets of stimuli can be easily parametrized. One example is a set of step-like pulses with the step height as a parameter. Choosing all stimuli from such a set enables one to express the firing criterion in terms of this parameter. The voltage-threshold concept will be the result. Other examples are given in the Discussion.

A natural stimulus for many cells in the brain is the EPSP bundle, i.e. a volley of EPSPs with some temporal dispersion. The stimulus time course in this case consists of the time courses of the single EPSPs. In an idealized set of stimuli, consisting of bundles composed of a fixed number of standard EPSPs, differing solely in their onset times, the onset times can be chosen as parameters in the set. In this case, it is natural to look for the firing criterion expressed in terms of those times. We solve the Hodgkin-Huxley (1952) equations with those stimuli to determine the combinations of onset times that lead to a spike. A constant potassium conductance is added to the original Hodgkin-Huxley equation to elucidate the role of inhibition in the process of selection of successful stimuli.

2.2 Standard unitary EPSP

An exact mathematical expression for the unitary EPSP (uEPSP) time course is derived on the basis of cable theory (Jack and Redman 1971; Redman and Walmsley 1983b). It is constructed as the convolution of two expressions:

$$EPSP(t) = \int_0^{t_{max}/\tau_M} f_\delta(t-\theta) f_\alpha(\theta)\, d\theta$$

The first expression is the Hodgkin formula for the function of a unit source in an infinite cable (Fatt and Katz 1951):

$$f_\delta(t) = \frac{1}{2\lambda C_{M1}\sqrt{\pi t}} \exp\left(-\frac{X^2}{4t} - t\right)$$

The second is the synaptic current time course:

$$f_\alpha(t) = Q\alpha^2 t \exp(-\alpha t)$$

Here t is dimensionless, τ_M = 10 ms, λ = 100 μm, X = 1.2, α = 50, $Q = 2.4 \times 10^{-14}$ C, $C_{M1} = 5 \times 10^{-2}$ μF/m. C_{M1} is the capacitance of a 1 m long nerve fibre.

Parameters in these formulae are chosen to fall into the set of waveforms observed in different neurons (Redman and Walmsley 1983b; Fetz and Gustafsson 1983; Andersen et al. 1987; Turner 1988). Finally, the EPSP (Fig. 1) has the following waveform parameters: 10%–90% rise time = 2.0 ms; τ_{peak} = 4.57 ms; halfwidth = 10.0 ms. The maximum EPSP value, V_{peak}, is 0.58 mV for NP = 100, and 0.058 mV for NP = 1000. The $EPSP(t)$ values are set to zero for $t \leq 0$, or $t \geq t_{max}$, where t_{max} is chosen to satisfy the inequality $EPSP(t_{max})/V_{peak} \leq 10^{-5}$, and is about 110 ms. The $EPSP(t)$ values are calculated in 1000 points distributed uniformly between 0 and t_{max}, and stored on hard disk. Values in the intermediate points are calculated by means of the linear approximation procedure.

Table 1. Values of inhibition potential V_{inh}, produced by additional conductance, g_{iK}, and corresponding values of n, m, h, taken as initial values for (2–5)

No	$g_{iK}/(m.mho/cm^2)$	V_{inh}/mV	n	m	h
1	0.000	0.00	0.318	0.0529	0.596
2	0.125	1.27	0.298	0.0455	0.638
3	0.256	2.53	0.280	0.0391	0.676
4	0.400	3.77	0.262	0.0336	0.711
5	0.580	5.04	0.245	0.0288	0.743
6	0.818	6.30	0.229	0.0246	0.772
7	1.178	7.57	0.214	0.0210	0.799
8	1.803	8.83	0.199	0.0179	0.825

2.3 Compound EPSP

The compound EPSP time course, $CompEPSP(t)$, originates from the summation of uEPSPs which start randomly within a time window W. To a first approximation, this summation is expected to be linear (Langmoen and Andersen 1983). Thus, the compound EPSP is calculated according to the following formula:

$$CompEPSP(t) = \sum_{k=1}^{NP} EPSP(t - t_k) \quad (1)$$

where t_k, $k = 1, \ldots, NP$ are random numbers in the interval $[0;W]$.

2.4 Membrane dynamics description

The membrane dynamics is calculated in accordance with the Hodgkin-Huxley equations for the membrane voltage, V (V = 0 at rest, depolarization negative), and the gating particle parameters n, m, h:

$$dV/dt = (-g_K n^4(V - V_K) - g_{Na} m^3 h(V - V_{Na}) - g_l(V - V_l) + I)/C_M - g_{iK}(V - V_K)/C_M \quad (2)$$

$$dn/dt = \alpha_n(1 - n) - \beta_n n \quad (3)$$

$$dm/dt = \alpha_m(1 - m) - \beta_m m \quad (4)$$

$$dh/dt = \alpha_h(1 - h) - \beta_h h \quad (5)$$

where

$$I(t) = -C_M dCompEPSP(t)/dt \quad (6)$$

Except for g_{iK}, all constants and the voltage dependences of the rate constants are taken from Hodgkin and Huxley (1952).

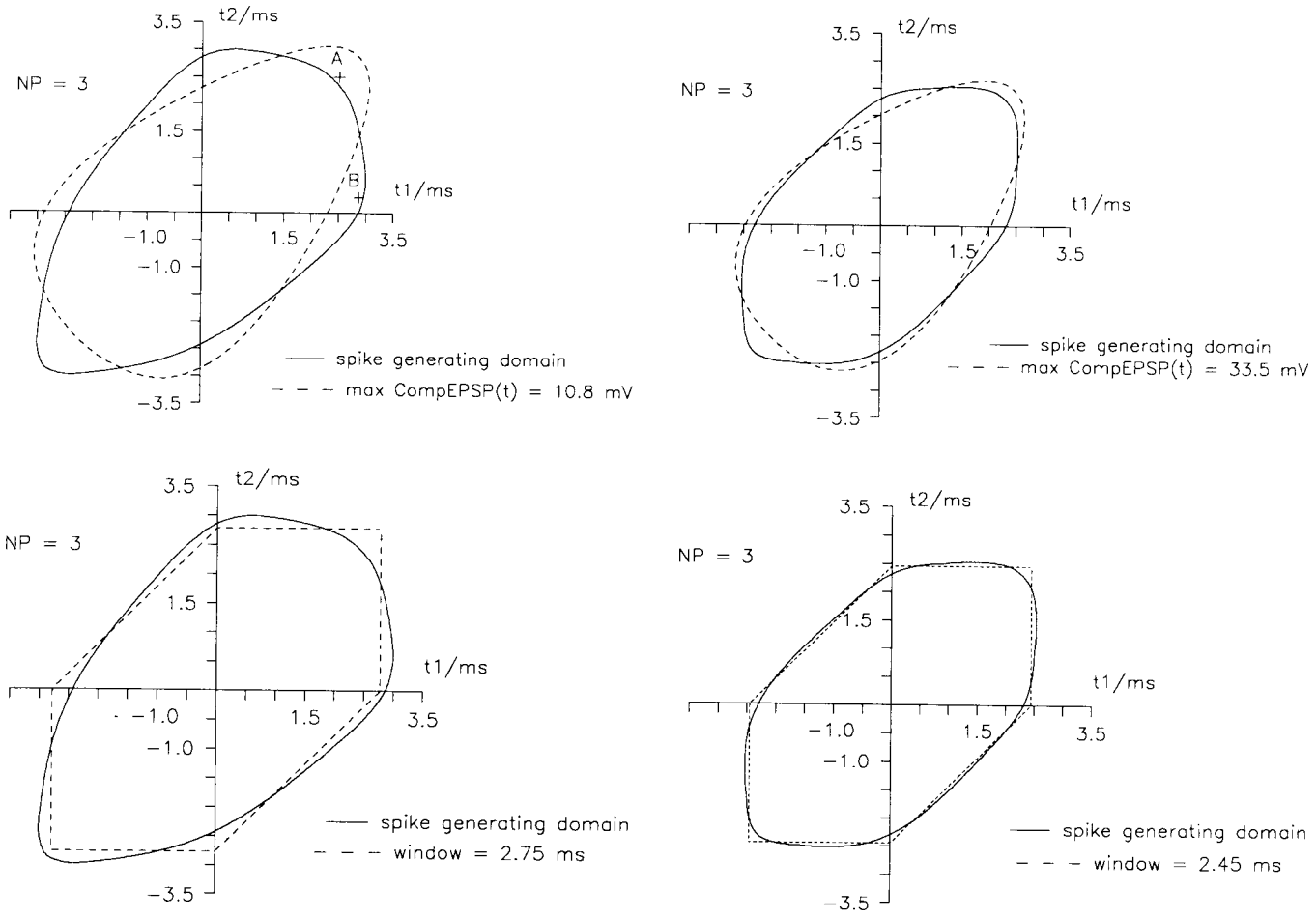

Fig. 2a–d. Comparison of the spike-generating domain with the equivoltage and window domains for stimuli composed of three EPSPs: $CompEPSP(t) = EPSP(t) + EPSP(t-t_1) + EPSP(t-t_2)$. Point (t_1, t_2) belongs to spike-generating domain if and only if the stimulus with onset times $0, t_1, t_2$ triggers an action potential. **a**, **b** Inhibition potential, $V_{inh} = 0$, $EPSP(t)$ has been scaled to $V_{peak} = 3.78$ mV. **c**, **d**: $V_{inh} = 5.04$ mV, $V_{peak} = 11.62$ mV

2.5 Inhibition paradigm

The extra term – the last term in (2) – is added to treat the effect of inhibition on the selection of successful stimuli. g_{iK} is expected to be time-independent and takes ten different values (Table 1). For the three largest values of g_{iK} spikes are suppressed at all values, and therefore only the smallest of the three is presented. For each g_{iK}, the system (2-5) is allowed to evolve freely ($I = 0$) from the state with $V = 0$ to a steady state with $dV/dt = 0$ during a time interval of about 30 ms. The V steady-state value is treated as the inhibition potential, V_{inh}, corresponding to the given g_{iK}. Together with the n, m, h steady-state values (Table 1), this value was taken as the initial value in each numerical experiment that models a response to a compound stimulus.

2.6 Algorithm outline

For each window W the set of NP random times, t_k, $1 \leq k \leq NP$, $0 \leq t_k \leq W$, within the window is generated (built-in random-number generator from Turbo Pascal 7.0, Borland International). The generator was preliminarily tested for randomness by calculating the first correlation function for series of 1000 trials. The membrane dynamics were run (Merson initial value problem algorithm from CERN FORTRAN Library, translated into Pascal) according to (2–6) with $CompEPSP(t)$ expressed by (1), and with the initial values taken from Table 1, during a time interval equal to W + 30 ms. If the depolarization exceeded 50 mV the trial was ended and was considered successful, because under this depolarization a full-scale action potential always develops.

3 Results

3.1 Test of the voltage-threshold concept for compound stimuli of three uEPSPs

Stimuli composed of three ($NP = 3$) EPSPs are considered first. Here the set of all stimuli can be parametrized by two onset times, t_1 and t_2. The third one is set to zero. From 5000 combinations of parameters (t_1,t_2), distributed uniformly within the domain $0 \leq t_1 \leq t_2 \leq 3.5$ ms, the successful and unsuccessful ones were determined.

This allows the spike-generating domain to be located within the whole coordinate plane of the parameters t_1, t_2, as shown in Fig. 2. We use the fact that if values t_1, t_2 are fixed, then six combinations of onset times – (t_1,t_2), (t_2,t_1), $(-t_1,t_2-t_1)$, $(t_2-t_1,-t_1)$, $(-t_2,t_1-t_2)$, $(t_1-t_2,-t_2)$ – give rise to the same $CompEPSP(t)$, and are equivalent in initiating a spike. For each pair (t_1,t_2), the maximum voltage, V_{max}, reached by the corresponding $CompEPSP(t)$ is also calculated. In Fig. 2 the spike-generating domain is compared with the domain where V_{max} is greater than or equal to a certain value, as well as with a fixed window domain. All three domains overlap to a large extent. Nevertheless, there are subdomains where $CompEPSP(t)$ has a larger maximum voltage but does not initiate a spike (point A in

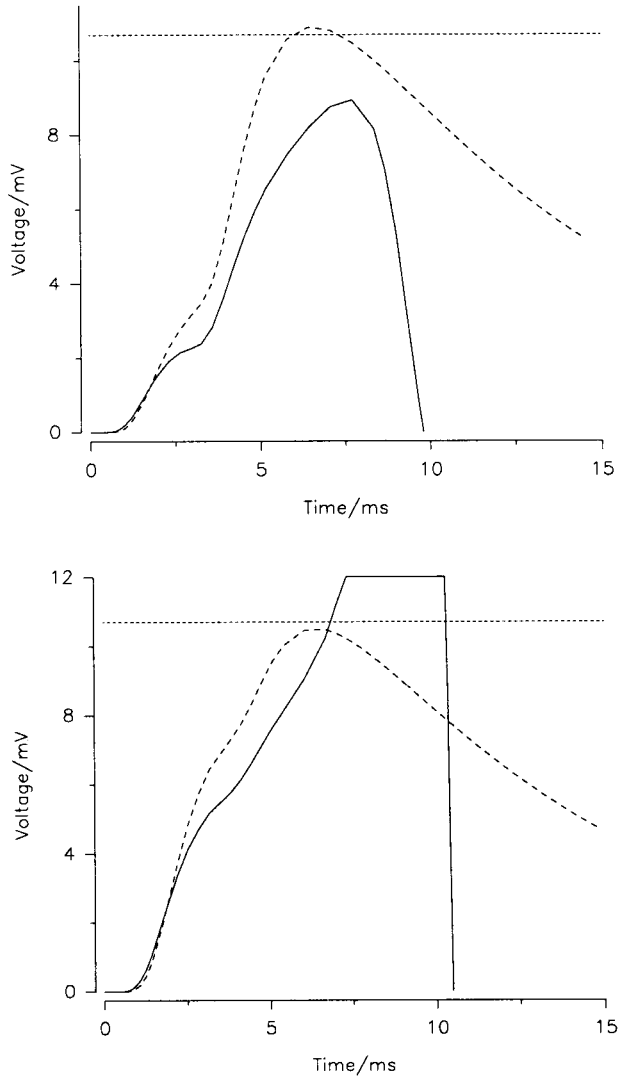

Fig. 3a,b. $CompEPSP(t)$ (*dashed line*), and $-V(t)$ (*continuous line*) time courses corresponding to points indicated in Fig. 2a. *Horizontal dashed line* indicates depolarization 10.7 mV. **a** Corresponds to point A in Fig. 2a: t_1 = 2.43 ms; t_2 = 2.43 ms; the stimulus maximum voltage, max $CompEPSP(t)$ = 10.90 mV. **b** Corresponds to B in Fig. 2a: t_1 = 2.91 ms; t_2 = 0.25 ms; max $CompEPSP(t)$ = 10.511 mV

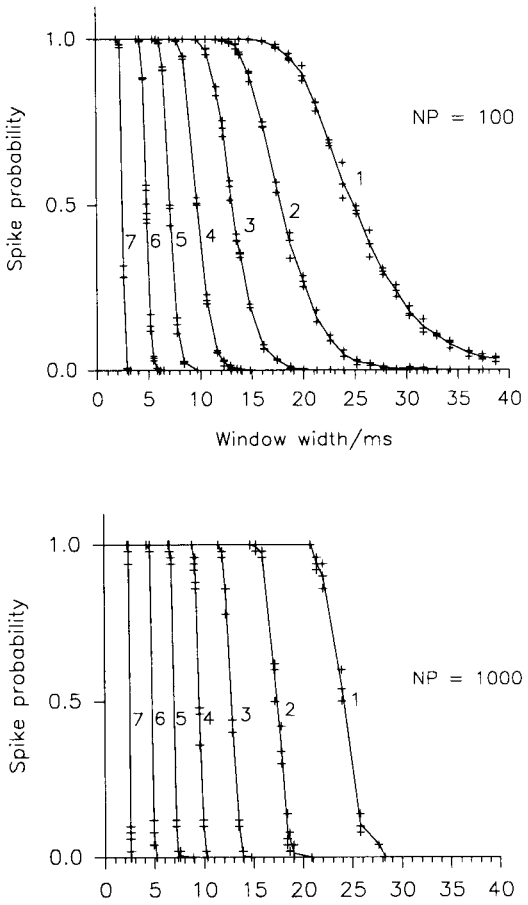

Fig. 4. Probability of triggerring of action potential by a compound stimulus (**a** NP = 100; **b** NP = 1000) versus width of the window from which all EPSPs start. Curve *numbers* correspond to rows in Table 1

Fig. 2a); also, $CompEPSP(t)$s with smaller V_{max} can initiate a spike (point B in Fig. 2a). Figure 3 shows the time course of the $CompEPSP(t)$ and V.

3.2 Multisynaptic stimuli

It is not possible to follow the above procedure if the CompEPSP is composed of a vast number of unitary stimuli, because the number of checking points grows enormously with the dimension of the parameter set. Also, the shapes of spike-generating and equivoltage domains in the multidimensional space of parameters are too complicated to be comparable. At the same time there appears a remarkable similarity between the spike and window domains in Fig. 2d, where the data for an inhibited neuron are presented. The width of time window the unitary stimuli start from represents a simple parameter labelling complex stimuli. By means of the Monte Carlo method it is possible to test it for the ability to discriminate between successful and unsuccessful CompEPSPs.

3.2.1 Time window concept. The compound stimuli composed of 100 and 1000 uEPSPs are considered. For NP = 100, V_{peak} is equal to 0.58 mV, as shown in Fig. 1, and for NP=1000, the uEPSP values are scaled to V_{peak}= 0.058 mV. To calculate the probability of a spike, $FP(W)$ for a given W, 500 trials are made for NP=100 and 50 trials for NP=1000. This ensures a precision of about 10% for FP values. (For compound stimuli with NP = 1000, fewer trials are required to obtain the same precision, because the dispersion of the time course of the stimuli is less in this case than for NP = 100).

The calculation is carried out for all ten inhibitions simultaneously. We assume that if at some level of inhibition the stimulus becomes successful, it must therefore be successful for all lower inhibitions, and that if it is unsuccessful, it remains unsuccessful for any higher level of inhibition. In preliminary experiments with a smaller number of trials, the points at which $FP(W)$ changes substantially are located,

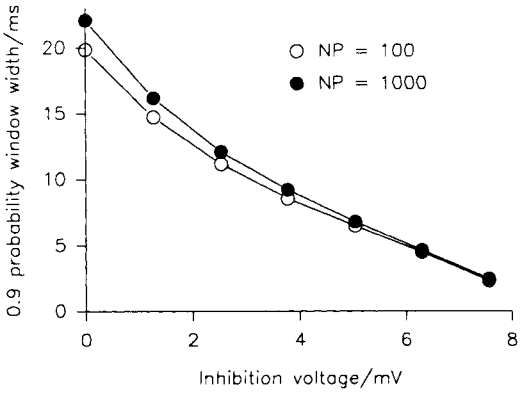

Fig. 5. Dependence of window width which causes a spike with a probability of 0.9, on the inhibition voltage

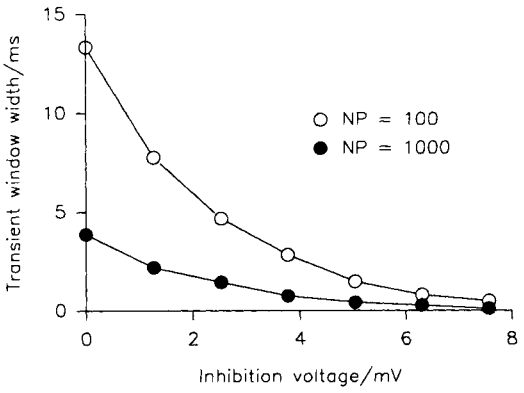

Fig. 6. Sharpness of the cut-off of non-coherent stimulations versus inhibition voltage. The transient window is the time window were $FP(W)$ changes from 0.9 to 0.1

and for the basic calculation the window values are chosen near these points. The data obtained are presented in Fig. 4. Each curve is calculated three times and the mean values plotted. The dependences obtained have a step-like character that suggests the threshold-type paradigm operates in selecting the successful stimuli.

Let $W(\alpha)$, where $0 < \alpha < 1$, denote the (unique) root of the following equation:

$$FP(W) = \alpha$$

We define the step location, W_S, as follows: $W_S = W(0.5)$. W_S strongly depends on the inhibition value, V_{inh}, and changes within a 25 ms interval when V_{inh} varies from 0 to 7.6 mV. This is shown in Fig. 5. The transient time window, W_T, is defined as follows: $W_T = W(0.1) - W(0.9)$. It also depends on V_{inh}. The data are presented in Fig. 6. For $NP = 1000$ and $V_{inh} = 7.6$ mV, W_S is equal to 2.5 ms and W_T to 0.11 ms. In this case the window threshold paradigm is satisfied with the precision of $W_T/W_S = 5\%$.

4 Discussion

The capability of compound stimuli to initiate a spike is investigated by means of the numerical solution of the Hodgkin-Huxley model. One may refer in this regard to some current developments of this model, in which additional membrane conductances and their non-uniform distribution between neuronal compartments are considered (Traub et al. 1992; Jaslove 1992). The Hodgkin-Huxley model is chosen here because, while relatively simple, it describes adequately the neuronal features essential for information processing, namely non-linearity, threshold-type behaviour, and the regenerative character of the response.

The set of compound stimuli is idealized: each stimulus is composed of a fixed number of the identical uEPSPs, with different onset times. The idealization is partially justified by the experimentally observed similarity between distally and proximally evoked EPSPs (Redman and Walmsley 1983a; Andersen et al. 1990). Additional calculations were made with faster and slower EPSPs (data not shown). In both cases, the step locations deviate slightly from the positions in Fig. 4, although qualitative and, to some extent, quantitative characteristics remain valid.

4.1 Voltage-threshold principle for stimuli with a gradual time course

Consider a set of one-component postsynaptic stimuli. Each stimulus in the set represents a single EPSP characterized by its own waveform. If all stimuli in the set are generated from a fixed (base) EPSP scaled to various peak voltages, then the voltage-threshold criterion must be appropriate for discrimination between successful and unsuccessful stimuli within the set, because V_{peak} adequately parametrizes that set.

On the other hand, suppose that a group of several uEPSPs with different waveforms were taken as basic when constructing the set of one-component stimuli. That means that each stimulus in the set is obtained by a proper scailing of a definite uEPSP from the group. On the basis of the preliminary numerical experiments, we may conclude that the pure voltage-threshold criterion seems to be inapplicable in such a set. This may explain, partially, the difficulties in formulating firing criteria exclusively in terms of membrane voltage (Kirkwood and Sears 1982; Fetz and Gustafsson 1983).

Consider a set of two-component stimuli. Each stimulus in the set is the sum of two fixed uEPSPs with different onset times. An adequate parameter here is the delay time between the first and second EPSPs. Thus, the selection of successful stimuli should be naturally based on the delay value. At the same time, the delay uniquely determines the maximum voltage, V_{max}, of the two-component stimulus, and vice versa. This being the case, V_{max} also looks like a good parameter, and selection of successful stimuli can be based on V_{max}.

On the other hand, in the experiments with real neurons, the action potential (AP) never begins at the peak value of a single EPSP (Coombs et al. 1955; Fetz and Gustafsson 1983). During the preliminary numerical experiments carried out in this study we were unable to choose the amplitude of the single EPSP such that AP development begins at the maximal voltage of the EPSP. On the contrary, if the AP appears, it starts well before V_{peak} is reached (data not shown).

As regards sets of stimuli with three (and more) components, the data in Figs. 2 and 3 suggest that V_{max} is not suitable for the precise discrimination between successful and unsuccessful stimuli.

4.2 The neuron as a time coherence discriminator

In a situation when several synaptic inputs act together, the neuron is treated as the coincidence detector. It is not easy, however, to define exactly the coincidence meaning even for two EPSPs, because they are practically zero during the first milliseconds after the onset and have a broad maximum and slow decay. In addition, it is not obvious which type of coincidence is relevant in the context of the information-processing tasks that higher neurons carry out. In some cases, a broad temporal integration is more relevant (Storm 1988). At the same time precise coincidence is absolutely improbable if the bundle is composed of hundreds of uEPSPs. The data in Fig. 4 suggest replacing the coincidence idea by a broader one. Namely, we may offer the degree of temporal coherence between inputs (measured as the inverse width of the time window from which all uEPSPs start) to be used instead of coincidence. The time-window idea has been discussed in connection with large-scale neuronal circuits (Damasio 1989a). The formulation of a firing criterion in terms of temporal coherence seems to be more appropriate in the context of experimentally observed synchronization in neuronal groups during sensory stimulation (Eckhorn et al. 1988; Gray and Singer 1989; Abeles et al. 1993).

At the same time it follows from Figs. 2 and 4 that a firing criterion based on temporal coherence is also not absolutely accurate. However, analysing the data in Figs. 2 and 4 we may expect the criterion to be fairly precise for an inhibited neuron with a reasonably large number of inputs.

4.3 Inhibition as binding controller at the single neuron level

The widely discussed phenomenon of feature binding during perception (Crick 1984; Sejnowsky 1986; Eckhorn et al. 1988; Damasio 1989b) seems to have a rudimentary representation at the single neuron level. Namely, if multiple inputs are coherent in time, the multisynaptic stimulation is interpreted in the neuron as originating from a single event. The degree of temporal coherence necessary to ensure such an interpretation can be effectively controlled by means of inhibition (Figs. 4, 5). In other words, the more inhibited the neuron is, the higher the degree of temporal coherence in the bundle that is required for treating it as a sign of a single event (object).

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