Numerical exploration of the influence of neural noise on the psychometric function at low stimulation intensity levels

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The relationship between stimulus intensity and the probability of detecting the presence of the stimulus is described by the psychometrical function. The probabilistic nature of this relationship is based on the stochastic behaviour of sensory neural channels and sensory networks involved in perceptual processing (Kiang 1968). This study tries to establish a continuum of variability across different levels of integration in the central nervous system. Once the opening and closing times of ionic channels was simulated, a threshold to the collective behaviour of voltage-gated ionic channels was imposed in order to generate the spike train of a single neuron. Afterwards, the trains of spikes of different neurons were added up, simulating the activity of a sensory nerve. By adding the activity due to the stimulus to the spontaneous neural behaviour, the psychometric function was simulated using a thresholding approach. The results can replicate the stochastic resonance phenomenon, but also open up the possibility that attentional phenomena can be mediated not only by increasing neural activity (bursting or oscillatory), but also by increasing noise at the neural level.

1. Introduction

This study attempts to deal with the question of how the stochastic nature of voltage-gated channels would influence the probability of event detection at low stimulation levels. In this sense, the study tries to join the probabilistic term included in the signal detection theory with its possible origin at the biophysical level in neurons related to perception. Previous studies have included noise with a neural origin as a fundamental component of the psychometric function, but these studies do not derive it directly from neural activity (Mortensen 2002).

The origin of electrophysiological neural activity is based on the input–output ionic currents in neural membranes mediated by ionic channels, chemically and voltage-gated. The behaviour of these channels follows probabilistic distributions that can be roughly approximated to an exponential probability distribution. Patch-clamp recording shows that this behaviour can be described as probabilistic: the probability of a channel to be opened or closed can be mathematically described, but the precise

instant when it would do so cannot be predicted (Hille 2001). In more formal terms, open dwelling times follow a simple exponential model, and closed channel interval times involve the sum of many exponential functions. Another important source of variability in neural activity comes from the quantal nature of liberation of synaptic vesicles in synapses after stimulation of the presynaptic terminals (del Castillo and Katz 1954; Destexhe *et al* 2001). In the case of light perception, the quantal nature of photon emission would be another source of variability. It can be supposed that the large number of channels and vesicles involved in the generation of the membrane potential could average these random influences. However, experimental evidence shows that membrane potential presents a clear fluctuation that can affect the generation of spontaneous action potentials (Strassberg and de Felice 1993; Chow and White 1996). Moreover, in physiological situations in which a relative steady input to the neurons can be supposed, the inter-spike interval distribution shows a broad variability (Gómez *et al* 1986, 1989). It has been proposed that the exact time in which a given spike is generated during

Keywords. Integration across levels; neural noise; probabilistic model; psychometric function; thresholding mechanisms

constant input stimulation reflects more the internal noise of the neuron than the inputs to the neuron (Schneidman *et al* 1998). It is generally accepted that the main source of neural noise lies in the synaptic transmission. However, the influence of voltage-gated channels in intracellular voltage fluctuations cannot be discarded (White *et al* 2000). The present simulation is based on voltage-gated channels around the axon hillock when the neurons are stimulated at a fixed intensity. Nevertheless, the inclusion of other sources of variability, such as synaptic input, would basically increase the level of neural noise at the axon hillock, the area in which the axon potential is generated.

Probabilistic description is also common at the psychological level, i.e. psychometric function reveals that the relationship of the intensity of the stimulus to obtain a perceptual threshold is described by an asymptotic sigmoid (Parker and Newsome 1998), indicating an asymptotic monotonic increase of the probability of perception as the intensity of the stimulus increases. The explanation for that would be based on the neural noise in the sensory channels, this noise being important when dealing with a low-intensity stimulus. Once the stimulus intensity is high enough, the probabilistic effects are negligible given that the stimulus is always over the perceptual threshold. Other behavioural examples in which a probabilistic description is well suited to empirical data description are ocular tremor, which is based on the random fluctuations of the abducens nerve motoneurons (Gómez *et al* 1989), the lever press response of rats during variable interval schedules of reinforcement (Gómez *et al* 1992a and 1992b), and the perceptual changes during observation of images in eye rivalry and ambiguous images (Gómez *et al* 1995). The latter three examples correspond to steady inputs and, therefore, the fluctuations can be attributed to internal fluctuations.

If the neural activity of individual neurons in steady-state can be described as probabilistic functions instead of deterministic functions, it is possible that the collective activity of neuron assemblies defining behaviour and perception could also be embedded in a probabilistic description as a consequence of the microscopically random behaviour of ionic currents around membranes. Therefore, these biophysical sources of variability would define the empirically observed statistical description of macroscopic perceptual psychometric function, indicating the conservation of noise from ionic channels to perceptual levels at low-intensity stimulation. The latter idea would also hold for other examples at the macroscopic level in which very high degrees of freedom can be observed.

Therefore, the aim of the present simulation study was to explain the probabilistic nature of psychometric function as a consequence of the random behavior of voltage-gated ionic channels. Specifically, the following rationale was followed: (i) the summing of individual realizations of a random process simulating the input currents does not abolish noise; (ii) if a threshold that simulates the action potential threshold is imposed, the need for a probabilistic description of the inter-spike interval remains; (iii) when computing the sum of several trains of spikes simulating the collective behaviour of a sensory nerve, a statistical description would be needed; (iv) and finally, if a threshold is imposed to define the number of spikes needed to reach the perceptual threshold, the psychometric function would be generated. The approach described in these four points would explain the probabilistic description of psychometric function at the perceptual level based on probabilistic functioning at the underlying biophysical levels.

It must be mentioned that this approach does not intend to capture all the intrinsically complex mechanisms occurring at the interior of neurons and neural assemblies, but the thresholding approach that holds for both action potential generation and perceptual threshold permits the exclusion of many of the details without losing the essentials. However, it would certainly be possible to produce much more detailed neural simulations using a neural software such as GENESIS (Bower and Beeman 1994). On the other hand, the influence of neural noise on the discharge of neurons (Schneidman *et al* 1998), and the influence of noisy spike trains on perception (Bruce *et al* 1999) have already been described. However, the conservation of noise from ionic channels to perception has not yet been addressed.

2. Simulations

2.1 *The summing of individual realizations of a random process simulating input currents does not abolish noise*

In order to simulate (matlab 7.0) the opening and closing of ionic channels, a Bernouilli random process of a totally independent series of numbers (0 for closed and 1 for opened) was generated, 0.5 being the probability for each event. Each individual number will be considered as an arbitrary time unit called bin. One of this series appears in figure 1A. The duration of opening (or closing) times had the characteristic exponential decay (figure 1B). The activity of many channels was generated and summed in order to simulate the overall contribution of statistically independent channels (given that we are dealing with excitation, no negative ionic input currents will be considered). The probability of opening a voltage ionic channel as a function of the voltage membrane is fitted by a sigmoideal function. In the present simulation this relationship was computed by means of a sigmoideal relationship between the number of opened channels and the stimulus intensity.

$$NOCH= TN* (1/(1+\exp(-INT))) \qquad (1)$$

NOCH = number of opened channels;
TN = total number of channels;
INT = intensity of stimulus.

In figure 1C, the series of opened channels per bin in 100, 300 and 1000 ionic channels are presented. Note that the increase in the number of opened channels is accompanied by an increase in variability. The frequency histogram distribution of the upper panel in figure 1C (representing the case for a neuron with 1000 channels, with a mean value of 500 opened channels) appears in figure 1D, and shows a bell-shaped distribution. The increase in variability with the number of opened channels is depicted in figure 1E, which shows a monotonic increase in standard deviation with the number of opened channels per bin. However, the variability when expressed in terms of coefficient of variation (standard deviation/mean) has a tendency to decrease with the dynamics similar to the square root of the number of opened channels (figure 1F). The same result was obtained when the membrane voltage was simulated with more realistic approaches (White *et al* 2000).

An important consideration that must be taken into account is that the neuron membrane, given its resistance–capacitance (RC) electrical characteristic, acts as a low-pass filter. Of course, it would decrease the voltage fluctuations but would not abolish them. Moreover, a membrane–time constant that is too high cannot be chosen (decreasing cut-off frequency) because, in that case, the speed of response of the neuron to an input would be greatly diminished.

2.2 *If a threshold simulating the action potential threshold is imposed, the need for a probabilistic description of the inter-spike interval remains*

The previous paragraph clearly shows that the number of channels opened for a fixed voltage presents considerable variability (figure 2A) and, therefore, the total current input to the neuron would also present a high variability. (The same result is obtained with a detailed physiological model of the neural membranes. *See* the discussion section and Steinmetz *et al* [2000].) In order to simulate the generation of action potentials, an arbitrary threshold was imposed on the signal reflecting the number of opened channels (i.e. input ionic current). As a consequence, a point process of 1 (above or equal to the threshold value) or 0 (below threshold) was generated simulating the timing of occurrence of the action potential (figure 2B). In such a thresholding situation, a geometrical distribution for the inter-spike time distribution is expected, given that each individual event has a probability q to be under the threshold and a probability p (p=1–q) of being above (or equal to) the threshold.

$$Pr (X = n) = (1-p)^{n-1} * p \qquad (2)$$

Therefore, the probability of a given inter-spike interval (X) to have a certain duration (n) is equal to the probability that the number of opened channels is above or equal to the threshold value in a certain time bin (p) multiplied by the probability that in the (n–1) previous time bins the number of opened channels was below the threshold value ($q=1-p$).

Figure 2C shows the frequency distribution of the inter-spike time intervals generated and the computed geometrical distribution. The geometrical distribution was computed from the parameters (mean and standard deviation of a geometrical distribution) extracted from the simulated data. The adjustment was improved by an iterative procedure on the p value (equation 2). Note the good fit between the computed geometrical probability distribution function and the simulated inter-spike intervals from the thresholding approach. A series of spike events were generated in order to add them to produce the collective behaviour of a sensory nerve (figure 2D). In the example shown in figure 2D, 30 neurons were simulated and the simulated spikes considered as a point process were added. In figure 2D (lower panel), the considerable variability in the number of spikes per time bin can be appreciated. This variable showed a bell-shaped distribution (figure 2E), which was similar to that obtained in the number of input channels per bin. The result of summing the spike series is then similar to the result of adding the number of opened channels in the simulated single neuron. In other words, the thresholding mechanism plus the summing of activity of many neurons replicate, in terms of variability, the number of opened channels. In some sense, the cycle of variability is regenerated when the pooled behaviour of a group of neurons is computed. The consequence is that when computing the sum of several trains of spikes simulating the collective behaviour of a sensory nerve, a statistical description would be needed (objective iii).

2.3 *If a thresholding mechanism is imposed on the number of spikes needed to reach the threshold perception, the psychometric function would be generated*

From the generated series of spikes, it is possible to compute the total number of spikes per bin for a given sensory nerve. In our case, the activity of a total number of 50 neurons with 120 input ionic channels was simulated. For this computation, the number of opened channels as a function of stimulus intensity was computed using a sigmoideal equation (equation 1). The result of this simulation is shown in figure 3. Our goal was to simulate the perception of stimuli of low intensity in order to compute the psychometric function and, given that perception probably depends on the activity of a population of neurons rather than on the activity of a
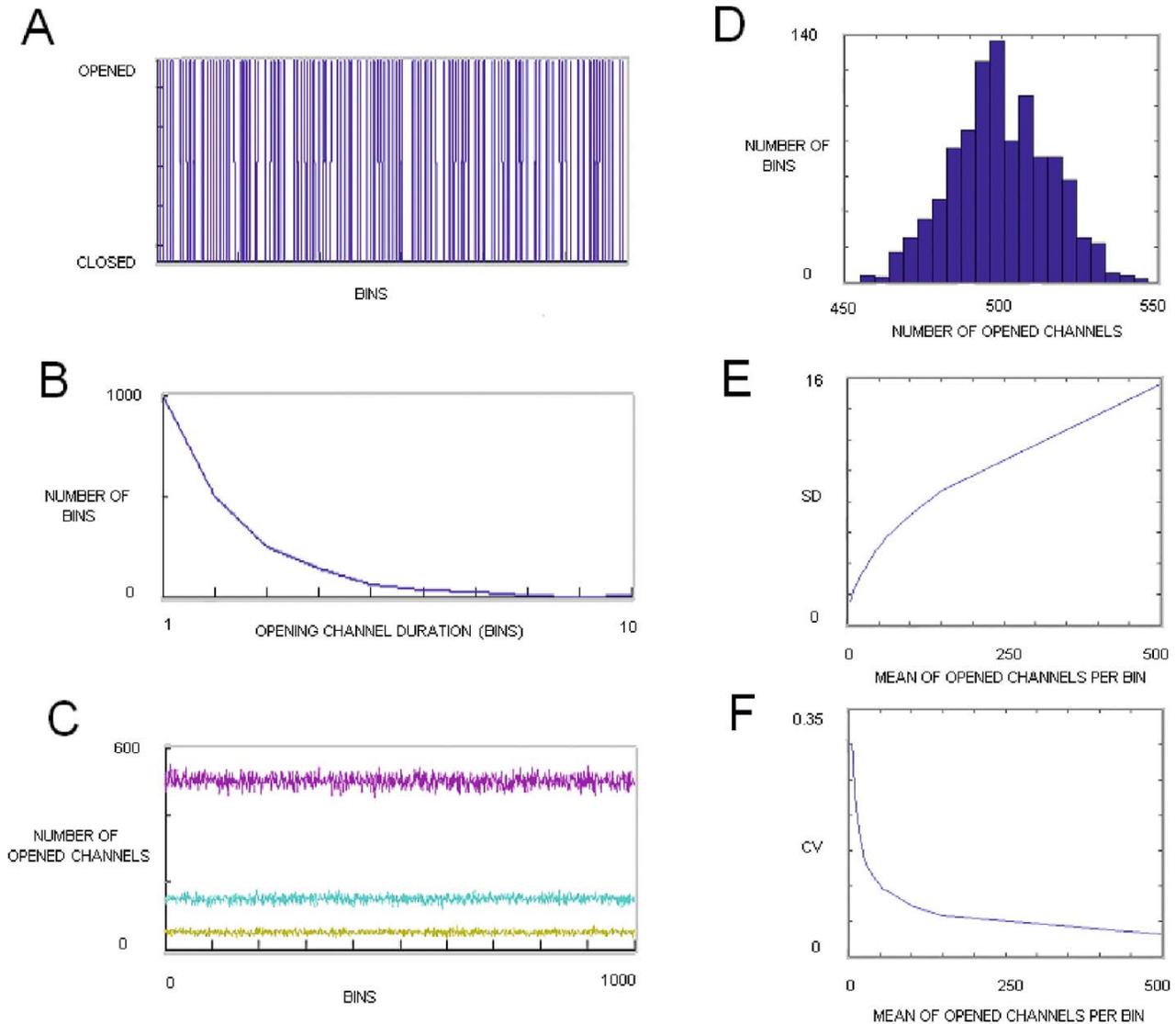
Figure 1. Simplified simulation of the opening–closing of ionic channels in individual neurons. (**A**) Series of openings and closings of an individual ionic channel. (**B**) Frequency histograms of the opening durations for an individual channel. Notice the exponential-like decay of the opening durations. (**C**) The number of opened channels per bin is displayed for a probability of 0.5 for opening and the complementary 0.5 for closing. The number of channels are 100, 300 and 1000. Notice that the increase in the number of opened channels is accompanied by an increase in variability. (**D**) The frequency distribution of the number of opened channels is shown for the case of 1000 channels. Notice the bell-shaped distribution. (**E**) Relationship between the mean number of opened channels and the standard deviation of the series, as those depicted in **C**. Notice the monotonic increase in variability when the mean increases. (**F**) On the contrary, the relative variability (coefficient of variation = SD/mean) decreases asymptotically with the mean number of opened channels.

single neuron, the number of spikes per bin in a group of 50 neurons was computed (figure 3A). Collapsing the spikes of 50 neurons does not change the important variability in the series that was obtained for the number of opened channels. Moreover, by increasing the intensity of the stimulation, an increase is produced not only in the number of spikes per bin, but also in the variability. In order to generate the psychometric function, the percentage of bins in which the value is higher than or equal to an arbitrary threshold was

computed for each stimulus intensity. Figure 3B shows the ability of the model to replicate standard psychometric function with its characteristic sigmoidal shape. The arrows indicate that reducing the threshold or injecting DC currents would produce a displacement of the psychometric function to the left, and that increasing the threshold would produce a displacement of the psychometric function to the right. Figure 4A confirms these expectations. If the threshold is reduced, there is a displacement of the psychometric
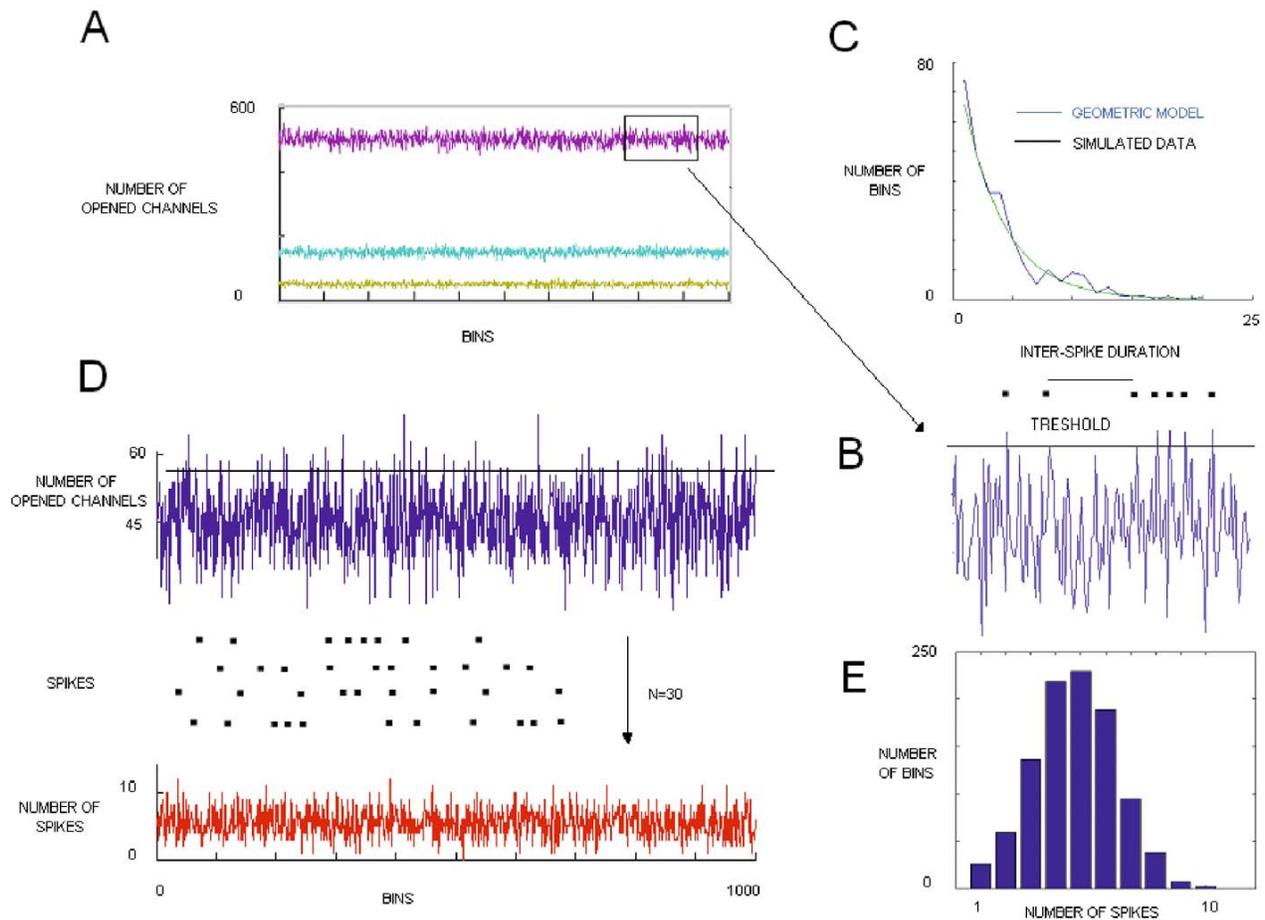
Figure 2. Simulation of the number of spontaneous spikes in a sensory nerve. (**A**) Same as in figure 1C. (**B**) A detail of the number of opened channels in each time bin. The line in the upper part indicates the hypothetical action potential threshold. The points above the line represent the generated spikes. (**C**) The frequency distribution of the inter-spike interval obtained and the computed expected distribution for a geometrical model are overlaid. Notice the good fit between the model and the simulated data. (**D**) From the number of opened channels (upper portion) and using the proposed thresholding approach (middle), the number of spikes of a sensory nerve can be computed (lower portion) (30 neurons simulated, the number of simulated channels per neuron is 100, and the probability of opening is 0.5). Notice the high variability of the generated series. (**E**) The frequency distribution of the numerical series in the lower part of (**D**), representing the activity of the sensory nerve, is displayed. Notice the bell-shaped distribution.

function to the left, indicating that the event detection level has been reached with a smaller amount of stimulus than in the standard condition. The opposite behaviour is obtained if the detection event threshold is increased. On the other hand, if a constant value (simulating DC injection) is added to the series representing the number of spikes, a displacement of the psychometric function to the left is also observed. This condition tries to replicate a situation in which it is possible to add to the neural activity derived from the stimulus and spontaneous activity, the external activation due to a direct current injected directly on the patch of cortex specialized in the analysis of the stimulus (Salzman *et al* 1992).

Another interesting situation to be simulated corresponds to the case in which a noisy signal is added to the series of spike number obtained by adding the activity of a group of neurons (spontaneous behaviour plus the stimulus intensity). When a series of normally distributed random numbers (mean = 0) was added to the series of collapsed number of spikes (figure 4B), a similar displacement of the psychometric function to the left was obtained. However, the displacement is different from that obtained in figure 4A, and increases with the magnitude of the standard deviation of added Gaussian noise. For low standard deviation Gaussian noise, the behaviour of the psychometric function is not very different from the standard psychometric function in
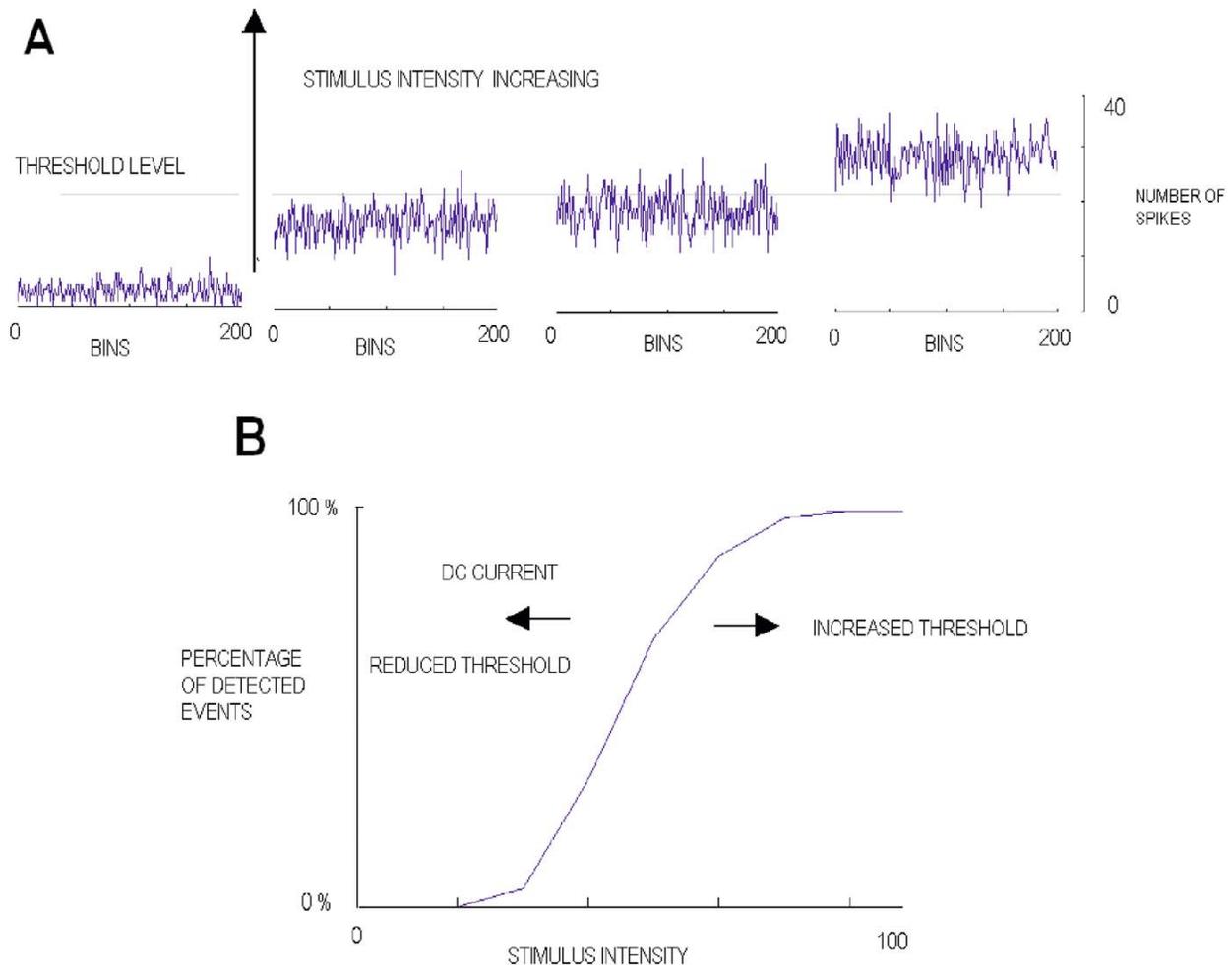
Figure 3. Computing of psychometric function. (**A**) The number of spikes summing the activity of 50 neurons with an increasing intensity of stimulation (computed by summing the series of number of spikes per bin, as in figure 2D) is displayed. The line shows the arbitrary threshold for the detection of events. The spikes generated by four different levels of stimulation with an increasing probability of opening of ionic channels are displayed. Notice that when the stimulus intensity is increased, the probability of reaching the threshold for the detection of events increases. Also notice that the variability in the number of spikes increases with the stimulus intensity. (**B**) Psychometric function obtained from different stimulus intensities. The arrow indicates the predicted displacement of function as a consequence of reducing or increasing the threshold for event detection or injecting a certain level of DC current.

the case when a DC current is injected. However, with a very high standard deviation, false alarms (responses to non-presented stimuli) can occur, as well as an increased number of misses (non-detected events). Therefore, the behaviour of the psychometric function when Gaussian noise is added can be summarized as: (i) increased detection at low noise intensities; and (ii) increased number of misses and increased false alarms at high noise levels. It must be remarked that, as indicated in the psychometric curves, there exists a certain value for the standard deviation of the Gaussian noise which allows an optimal performance (low Gaussian noise in figure 4B). This value of standard deviation would correspond to the stochastic resonance phenomenon. The relationship between the standard

deviation and the percentage of false alarms in the present simulation is shown in figure 5.

3. Discussion

The aim of this report was to demonstrate that the probabilistic nature of psychometric function could lie in the stochastic nature of the closing–opening pattern of voltage-gated ionic channels, without discarding other possible sources of variability at the biophysical level. Our simulations show that variability at the microscopic level can be conserved at the event detection level (perceptual level). The plausibility of the numerical simulations was
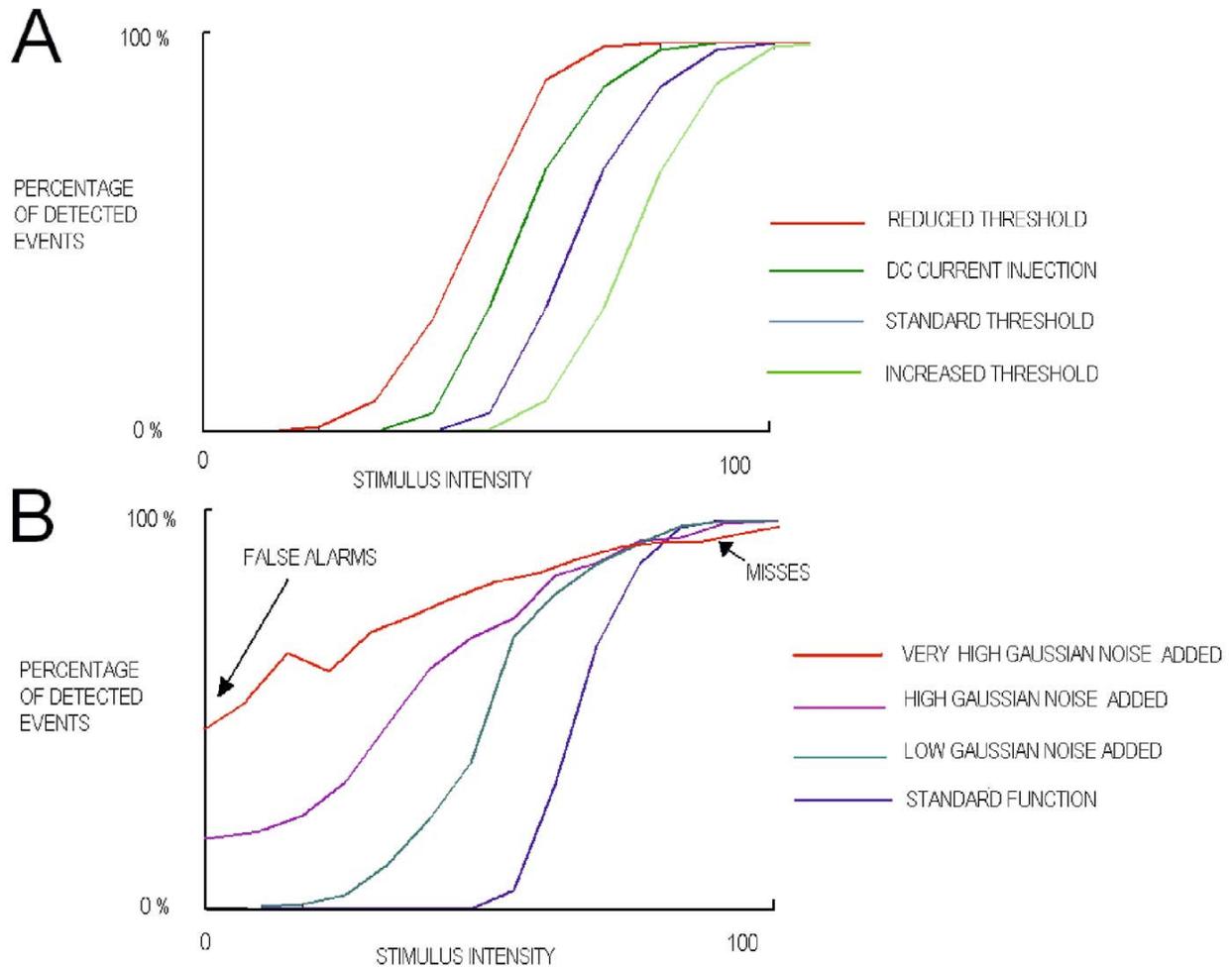
Figure 4. (**A**) Psychometric function in different conditions: in standard conditions, imposing a reduced or increased threshold for event detection and supposing a Direct Current (DC) activation on the network generating the detection of events. Notice that the effect of these changes basically displaces the psychometric function but does not change its shape. (**B**) Psychometric function in different noisy conditions: in standard conditions and in three different levels of zero–mean Gaussian noise. Notice that adding noise produces a flattening of the psychometric function with respect to the standard condition, and that the probability of detection is increased for low-intensity stimulation. However, false alarms can occur for high levels of noise. Moreover, very high noise levels produce a decrease in the probability of detection by increasing the number of misses (compare the red line with the blue line). The condition that would allow the phenomenon of stochastic resonance is the addition of a moderate amount of Gaussian noise.

validated by the properties of the simulated psychometric function in different conditions. The model generates certain predictions that offer pathways for empirical validation.

The main difficulty in interpreting our results arises from the lack of detailed neural biophysical elements in the present simulation. However, going from the level of dynamics of input ionic channels to the perceptual level in a detailed form seems to be an unrealistic approach. In spite of the huge amount of physiological data accumulated about the neural mechanisms of perception, the lack of knowledge of all these details is equally impressive. There are only a few cases where there is enough physiological

evidence to allow us to compute the total collective activity of a macroscopic structure (Shadlen *et al* 1996; Gómez *et al* 1989). However, even in those cases, the approach is from the neural discharge of action potential to the pooling activity of a macroscopic structure. This is not the case in this report, the aim of which was to prove that there is a conservation of noise across integration levels in the nervous system, from noise in ionic channel activity to the perceptual level. Therefore, the validation of the simulations would arise from the similarity of simulations with psychometric function, but also from the role of the proposed thresholding mechanism and from the central limit theorem (discussed
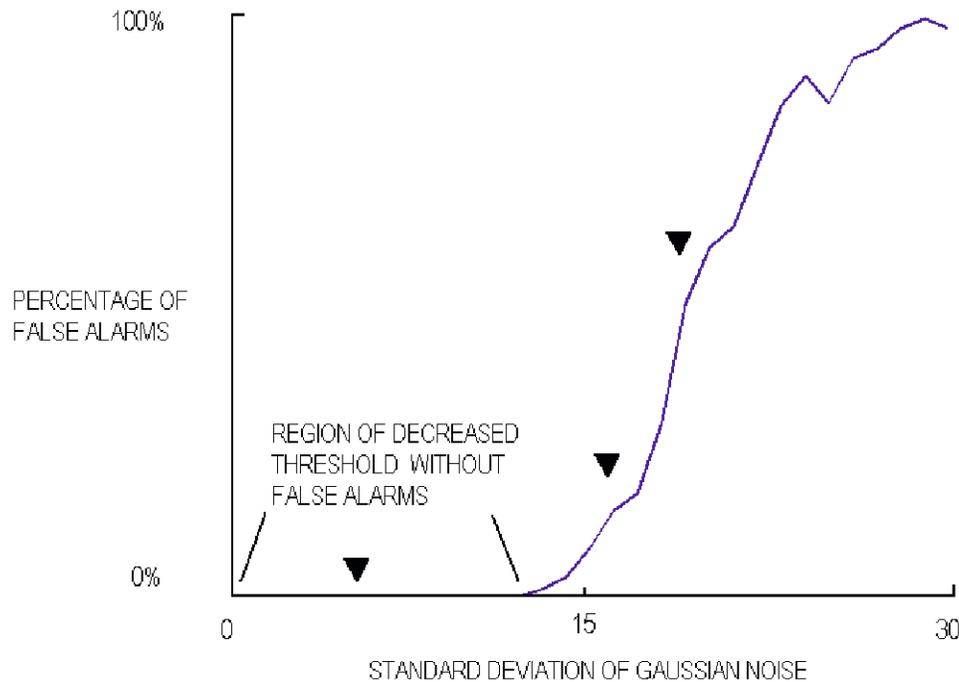
Figure 5. Percentage of false alarms vs the standard deviation of the added noise. Notice the increase in false alarms as the added noise increases. The triangles indicate the standard deviation of added noise that was used in the simulations in figure 4B. Notice that the percentage of false alarms corresponded to the intersection of the psychometric function with the Y axis (that corresponds to the zero stimulus condition). Finally, the presence of a region in which noise can be added without producing false alarms must be mentioned. This region would correspond to the area in which the stochastic resonance is operating.

later). One of the reasons that allows us to have confidence in the present simplified approach comes from the use of the thresholding approach. The use of a thresholding approach implies that equal to/above the threshold level, an event is produced (with a probability p) and below the threshold level, no event is produced (with a probability $q=1-p$). It defines a geometrical inter-event distribution, regardless of the type of probability distribution to which the threshold is applied (i.e. the statistical characteristics of the noise). With this approach, the type of random probability distribution on which the thresholding approach is applied can be considered to be relatively irrelevant.

Some of the results obtained in the present simulation at the neuronal level are similar to those obtained with a much more detailed description of the biophysical characteristics of neurons (Steinmetz *et al* 2000). In the simulations presented by Steinmetz *et al* (2000), subthreshold voltage fluctuations increased with the mean voltage, and the neuronal noise was normally distributed. In our simulation, the standard deviation of the series of the number of opened channels per bin increased monotonically with the mean number of opened channels (figure 1E). Moreover, the frequency distribution of the series of the number of opened channels per bin was bell-shaped. These two results are consistent with the results of subthreshold voltage membrane fluctuations,

using a much more detailed biophysical simulation by Steinmetz *et al* (2000). Another validation of our results is provided by the reduction in the coefficient of variation of membrane currents with the square root of the number of channels (figure 1F). This has been previously described by White *et al* (2000).

Steinmetz *et al* (2000) proposed that such fluctuations could have an impact on the precise timing of spike generation under natural or experimental inputs. In some cases, the subthreshold fluctuations could reach the threshold value and generate spontaneous spikes. In such situations, but also in conditions in which a constant input is added to a subthreshold noise, geometrical distributions should be expected for the inter-spike distributions, as was obtained in our simulation (figure 2C). If a deterministic constant input is added, the threshold would be reached more easily, but the inter-spike geometrical distribution would be maintained. In naturalistic situations where a constant input is delivered on the neurons, the inter-spike distributions obtained are of different types; they could be normally distributed (Gómez *et al* 1986) or follow a Poisson distribution (Gummer 1991; Richter *et al* 1996) and, in general, appear as unimodal left-skewed distributions (Barlow *et al* 1971). Given that after an action potential there are profound changes in ionic conductance, producing phenomena such as after-

hyperpolarization and adaptation, but also producing recurrent activities through reverberant circuits, it is not surprising that different empirical inter-spike frequency distributions are obtained when a constant input is applied to neurons. The inter-spike time distribution obtained in this report is very similar to that obtained by Lowen *et al* (1999), although they included reduction of firing probability due to after-hyperpolarization. However, for the purpose of this report: (i) the main source of variability in the inter-spike intervals is due to the neural noise based on the probabilistic nature of ionic currents (Steinmetz *et al* 2000), and (ii) the summing of the spikes of different neurons would produce a normally distributed series (figure 2D, and Gómez *et al* 1989) in which the stochastic nature of the pooled activity of neurons is preserved. The latter result is a consequence of the central limit theorem. The theoretical importance of the stochastic behaviour of spike trains under constant stimulus (due to biophysical noise) is that, regardless of which inter-spike distribution explains the numerical series of inter-spike time, the summing of a sufficient number of series would converge to a normal distribution (central limit theorem). It must be mentioned that in this report we are not dealing with recurrent activity in networks as probably occurs in associative cortical networks, which would produce a more predictable sequence of action potentials (Ikegaya *et al* 2004).

We can conclude that summing of the number of spikes of parallel axons of neurons submitted to a constant input (as constant as it can be) is highly variable and corresponds to a normally distributed probabilistic process. The same result has been previously obtained in a simulation of the total output of the auditory nerve when stimulated by a single pulse (Bruce *et al* 1999). If we assume a new fixed threshold level (a certain number of counted spikes), the psychometric function could be computed and then its probabilistic nature would be a direct consequence of noise at the neural membrane level. The sigmoidal shape of the psychometric function obtained is similar to the experimentally obtained functions in a plethora of psychophysical experiments. Some classic reports are those by Hecht *et al* (1942) and Johansson and Vallbo (1976). Simulation is able to predict the fact that reducing the threshold would produce a displacement of the psychometric to the left and, interestingly, direct current injection would bias psychometric function to lower stimulus intensities, as has been experimentally shown (Salzman *et al* 1992).

Another interesting property that allows validation of the simulation model is the reduction of threshold due to the addition of a noisy signal. This perceptual improvement is similar to the well reported process of "stochastic resonance". This concept refers to the fact that the addition of an optimal amount of noise leads to better information transmission (Moss *et al* 2004). In perceptual systems, it has been proved

that the addition of a certain amount of external noise to the stimulus reduces the perceptual threshold (Zeng *et al* 2000). The results of the present simulation show the same patterns for psychometric function (figure 4B), indicating its sensitivity to the stochastic resonance phenomenon. It must be remarked that the parameters of the added noise must be optimized to obtain stochastic resonance. In fact, the zero mean noise was able to reduce exclusively the ability to detect events for only low levels of Gaussian noise, and not for high levels of noise which, in fact, produces an increase of false alarms and misses. The conditions of signal-to-noise ratio that must occur to produce the stochastic resonance phenomenon are therefore dependent on the interaction of internal, external noise and the stimulus intensity level. As in our simulation, the increase in zero–mean noise would be derived from external or internal sources; the possibility that the improvement in detecting low-intensity stimulation (Hawkins *et al* 1990), which has been attributed to attention and therefore to increased neural activity (bursting or oscillatory), could also be due to an increase in biophysical neural noise can be proposed. The increase in zero–mean internal neural noise would produce the same effect as stochastic resonance when the noise is added from external sources.

The main source of variability of spike trains would arise from the probabilistic opening and closing of ionic channels. Given that other sources of noise exist in the neuron as synaptic noise or stochastic behaviour of the sensory stimulus itself, variability is an inner property of neural function and, given that summing up the spike trains does not eliminate noise, the conservation of stochastic properties from the biophysical level at neural membranes to perceptual levels can be proposed. However, in the present simulations, we deal only with excitatory activity. The addition of inhibitory noisy inputs would favour the convergence to more neural stable behaviour.

In summary, the present simulation can be validated by its ability to simulate the following results:

- Reproduction of the exponential close–open dynamics of ionic channels (Hille 2001).
- Normality and SD vs mean of input currents (number of opened channels). If the capacitative term of the neural membrane is not considered, the input current allows computation by Ohm's law of the intracellular voltage, which has been demonstrated to follow the normality and mean vs SD relationship as described in the present report (Steinmetz *et al* 2000).
- Reproduction of noisy spike trains (Barlow *et al* 1971; Gómez *et al* 1986; Gummer 1991; Richter *et al* 1996).
- The summing up of spikes is also a noisy Gaussian signal, as has been described for the abducens nerve in the oculomotor system, in which the properties of all neurons are known and, therefore, it is possible

to describe the macroscopic properties of the nerve (Gómez *et al* 1989).

- Reproduction of the sigmoidal shape of psychometric function as a consequence of the collective behaviour of sensory modules (i.e. Bruce *et al* 1999).
- The possibility of increasing the perceptual sensitivity as demonstrated by the displacement of psychometric function to the left. This point can be understood in terms of direct current injection as in the experiments by Newsome's group (Salzman *et al* 1992).
- The ability of the model to generate the stochastic resonance property by increasing the noise level of the sensory system (Zeng *et al* 2000; Moss *et al* 2004). An interesting property is that the standard deviation of Gaussian noise must be optimized in order to obtain the stochastic resonance phenomenon.

In addition to the neural and psychological plausibility, as described in the previous paragraph, the model is able to generate predictions that can be empirically tested. An interesting prediction, in order to empirically validate the proposed model and which can be tested by psychophysical experiments, is that for a fixed stimulus of low intensity, the time intervals between two perceived stimuli should follow a geometrical distribution.

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