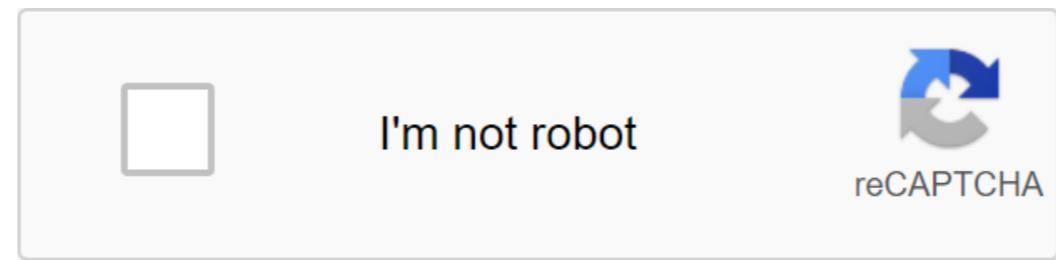


Why does frequency of action potentials increase when the stimulus intensity increases



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Neural Action Potential - Frequency coding in the nervous system We stressed that once depolarization caused by a stimulus above the threshold, the resulting neuronal action potential is full of action potential (i.e., it's all or nothing). If the stimulus power is increased, the size of the action potential does not get larger (see figure). If the size (i.e. amplitude) of action potential is always the same and does not depend on the size of the stimulus, then how then the nervous system code the intensity of the stimulus? The trick that the nervous system uses is that the stimulus force is encoded in the frequency of action potentials that are generated. Thus, the stronger the stimulus, the higher the frequency at which action potentials are generated (see Figure 1 and 2 below). So we say that our nervous system is frequency-modulated, not amplitude modulated. The frequency of potentials is directly related to the intensity of the stimulus. Given that the frequency of potentials is determined by the force of stimulus, the plausible question to ask is, what is the frequency of potentials in neurons? Another way to ask this question is how much action potential can a neuron generate per unit of time (such as action potential per second)? Physiologically, the potential action of frequency up to 200-300 per second (Hz) is regularly observed. There are also higher frequencies, but the maximum frequency is ultimately limited to an absolute fire-resistant period. Since the absolute fireproof period is 1 ms, there is a limit to the highest frequency at which neurons can respond to strong stimuli. This means that the absolute fireproof period limits the maximum number of action potentials generated per time by axon. As described earlier, the strength of the stimulus should be very high in order to ensure that the duration of the action potential is as short as the duration of an absolute fire-resistant period. Overcoming the relative refractory period requires a stronger-than-usual stimulus (see Fireproof Periods for review). Since the absolute fireproof period can last from 1 to 2 ms, the maximum frequency reaction is 500-1000 with 1 (Hz). The sample calculation is shown below with the assumption that the absolute fireproof period is 1 ms in duration. Eq. 1 Cycle here refers to the duration of an absolute fire-resistant period, which, when the strength of the stimulus is very high, is also the duration of the potential. Similarly, if the absolute fireproof period of the neuron is 2ms, the maximum frequency will be 500 Hz, as shown below. Eq. 2 Figure 1. Frequency coding in the nervous system: Threshold stimulus. If the threshold stimulus is applied to the neuron and maintained (upper, red), the potential of action occurs with maximum frequency, which is limited to the amount of absolute and relative fire-resistant periods (bottom, blue trace). In here incentive incentive to this, which is just strong enough to bring the resting neuron to the threshold. Thus, with the retained threshold, the subsequent potential for action arises only at the end of the relative fire-resistant period of the previous action. The upper and lower footprints are in the same timeline. The dotted line represents a threshold voltage (Vthreshold) of about 50 mV. ARP, absolute fireproof period; RRP, relative fire-resistant period. The above calculations correspond to the maximum frequency of action potentials and will be present only if the stimulus is very large to overcome the relative fire-resistant period. Thus, the maximum frequency of potentials is ultimately limited by the duration of an absolute fire-resistant period. On the other hand, if the stimulus is large enough to bring the neuron to the threshold at rest, the maximum frequency of action potentials will now be governed by the total duration of the fire-resistant period of the neuron (i.e. the amount of absolute and relative fire-resistant periods) (see Figure 1). In a typical neuron, it's 1 and 4 and 5ms. Under this condition, the maximum frequency of action potentials is 200 Hz, as shown below: Eq. 3 Here the cycle refers to the full duration of the potential of action (absolute fire-resistant period · relative fire-resistant period). Figure 2. Frequency coding in the nervous system: super-threshold stimulus. If the pressure stimulus is applied to the neuron and is maintained (upper, red), the potential of action is not allowed to complete the relative fireproof period (bottom, blue trace). Thus, with retained pressure stimulation, subsequent action potentials arise during the relatively fireproof period of the previous potential of action. With the increase in the strength of the stimulus, subsequent action potentials occur earlier during the relative fireproof period of previous action potentials. With very strong stimuli, subsequent action potentials occur after the completion of the absolute fireproof period of the previous action potential. Thus, the maximum frequency of potentials is ultimately limited by the duration of an absolute fire-resistant period. The upper and lower footprints are in the same timeline. The dotted line represents a threshold voltage (Vthreshold) of about 50 mV. ARP, absolute fireproof period; RRP, relative fire-resistant period. Published: Thursday, July 5, 2012 Last update: Friday, January 17, 2014 Decided rimonosty Exercise 3: Neurophysiology of Nerve Impulses: Activity 6: Action Potential: Coding for Stimulus Intensity Laboratory Report Preliminary Lab Quiz Results You scored 100%, answering 4 of 4 questions correctly. Time after potential action, when the potential of the second action can be created only if the intensity of the stimulus increases You correctly answered: c. relative fire-resistant period. The term frequency refers to you correctly answers: c. the number of potential actions per second. The purpose of this activity is to investigate you correctly answered: b. the link between the intensity of the stimulus and the frequency of action potentials. You haven't completed the experiment yet. Experiment data: You scored 100% of the results after the lab quiz, correctly answering 4 of the 4 questions. If the interval between the action potentials (interspicial interval) is 0.1 (1/10) seconds, what frequency of action potentials will be observed? You correctly answered: c. 10 Hz With a long-term stimulus, which is slightly higher (more depolarized than) threshold, you expect to receive additional action potentials when the membrane is completed You correctly answered: b. absolute and relative fire-resistant periods. What of the following changes occurs when you increase the intensity of the stimulus? You correctly answered: c. The frequency of potentials is increasing. The absolute fireproof period is about 3.75 msec. What intensity of the stimulus will produce the potential of action with this interval interspike? You correctly answered: d. None of these incentives will produce the potential of action at such a high frequency. Review sheet Results Why are several potential actions generated in response to a long stimulus that is above the threshold? Your answer: a long stimulus that is above the threshold occurs the potential of action after a relative fireproof period. Why does the frequency of potentials increase when the intensity of the stimulus increases? How well do the results compare to your forecast? Your answer: They are interactive. Despite the enormous complexity of the brain, one can get an idea of its function by paying attention to two main details: first, the ways in which individual neurons, components of the nervous system, are connected together to create behavior. Second, the biophysical, biochemical and electrophysiological properties of individual neurons. A good place to start with the components of the nervous system and how the electrical properties of neurons endows nerve cells with the ability to process and transmit information. 1.1 Introduction to potential action Figure 1.1 Click colored circles (easy stimulus) to activate. Theories of coding and transmission of information in the nervous system return to the Greek doctor Galen (129-210 AD), who proposed a hydraulic mechanism by which muscles contract because the fluid flows into them from hollow nerves. The basic theory was and was additionally developed by René Descartes (1596 - 1650), who suggested that animal spirits flowed from the brain through the nerves and then into the muscles to produce movements (see this animation for a modern interpretation of such hydraulic theory for neural function). A major paradigm shift occurred with the groundbreaking work of Luigi Galvani, who discovered in 1794 that the nerve and muscles could be activated by charged electrodes and suggested that the nervous system functioned by electrical signaling. However, there was a debate among scientists whether electricity was in the nerves and muscles or whether the nerves and muscles were simply responding to harmful electric shocks through some internal nonelectric mechanism. This issue was not resolved until the 1930s with the development of modern electronic amplifiers and recording devices that allowed electrical signals to be recorded. One example is H.K. Hartline's groundbreaking work 80 years ago on electrical signaling in the horseshoe crab of the Limulus. Electrodes were placed on the surface of the optic nerve. (By placing electrodes on the surface of the nerve, you can get an idea of the changes in the membrane potential that occur between the outer and inner parts of the nerve cell.) Then 1 s duration flashes of light of varying intensity were presented in the eyes; first dim light, then brighter lights. Very dim lights have not produced any change in activity, but bright lights produced small repetitive spikes as events. These bursts are like events called potential action, nerve impulses, and sometimes just spikes. Action potentials are the main events that nerve cells use to transmit information from one place to another. 1.2 Features of the Action Potentials Of the entries in the figure above illustrate three very important features of neural action potentials. First, the potential for nervous action has a short duration (about 1 msec). Second, the nerve potentials of the action are triggered in all or nothing fashion. Third, nerve cells encode the intensity of information by the frequency of potentials. When the intensity of the stimulus increases, the size of the action potential does not increase. Rather, the frequency or number of action potentials increases. In general, the greater the intensity of the stimulus, (whether it's an easy stimulus for a photoreceptor, a mechanical stimulus to the skin, or a stretch on the muscle receptor) the more potential the action is caused. Similarly, for the motor system, the greater the number of action potentials in the motor neuron, the greater the intensity of muscle contraction, which is innervated that the motor is a neuron. Action potentials are important for the functioning of the brain, as they spread information in the nervous system to the central nervous system and spread the commands initiated in the central nervous system to the periphery. Therefore to understand their properties thoroughly. Who to who questions about how the potentials of action are both initiated and spread, we need to write down the potential between internal and external nerve cells using intracellular recording techniques. 1.3 Intracellular recordings from neurons The potential difference between the membrane of nerve cells can be measured using a microelectrode, the tip of which is so small (about micron) that it can penetrate the cell without producing any damage. When the electrode is in the bath (extracellular environment) there is no potential registered because the bath is isotropic. If the microelectrode is carefully inserted into the cell, the potential changes dramatically. Reading the voltmeter instantly varies from 0 mV to read the potential difference of -60 mV inside the cell relative to the outside. The potential that is recorded when a living cell is pierced by a microelectronic is called resting potential and varies from cell to cell. It shows that -60 mV, but can range from -80 mV to -40 mV, depending on the specific type of nerve cells. In the absence of any stimulation, the potential of rest is usually constant. You can also write down and explore the potential of action. Figure 1.3 illustrates an example in which a neuron is already punctured by a single microelectrode (recording electrode). It is connected to a voltmeter. The electrode fixes the potential of rest -60 mV. The cell was also punctured by a second electrode called a stimulating electrode. This electrode is connected to the battery and the device that can control the amount of current (I) that flows through the electrode. Changes in the membrane potential are made by closing the switch and systematically changing both the size and polarity of the battery. If the negative battery pole is connected to the inner cell, as in Figure 1.3A, an instant change in the amount of current will pass through the stimulating electrode, and the membrane potential becomes transiently more negative. This result should not come as a surprise. The negative battery pole makes the inner cell more negative than it used to be. Changing the potential that increases the polarized state of the membrane is called hyperpolarization. The cell is more polarized than usual. Use an even bigger battery, and the potential becomes even greater. As a result of hyperpolarization, the graded functions of the values of the stimuli used to produce them. Now consider the case where the positive battery pole is connected to the electrode, the cell's potential becomes more positive when the switch is closed (Figure 1.3B). Such potentials are called depolarizations. The polarized state of the membrane is reduced. Larger batteries produce even greater depolarization. Again, the magnitude of the responses is proportional to the size of the incentives. An unusual event occurs when the amount of depolarization reaches a level of membrane potential called a threshold. A whole new type of signal is initiated; potential action. Note that if the battery size increases even more, the amplitude action potential is the same as the previous one (Figure 1.3B). The process of obtaining the potential of action in the nerve cell is similar to the ignition of the fuse with the source of heat. A certain minimum temperature (threshold) is required. The temperature below the threshold does not ignite the fuse. The temperature above the threshold ignites the fuse as well as the threshold temperature, and the fuse does not burn brighter or hotter. If you squander the current stimulus long enough, however, train action potentials will be triggered. Overall, the potential action will continue to shoot as long as the stimulus continues, with the frequency of firing proportional to the magnitude of the stimulus (Figure 1.4). The potential actions are not only initiated in all or nothing, but they are also spread in an all or nothing way. The potential of action initiated in the cell body of the motor neuron in the spinal cord will be spread in a non-profile way in any case to the synaptic terminals of this motor neuron. Again, the situation is similar to a burning fuse. As soon as the fuse ignites, the flame will spread to the end. 1.4 Action Potential Components consists of several components (Figure 1.3B). A threshold is the value of membrane potential which, if achieved, leads to the initiation of all-or-nothing action potential. The initial or upward phase of the action potential is called depolarization or recovery. The range between 0 mV and peak amplitude is an excess. The return of membrane potential to the potential of rest is called the repolarization phase. There is also a phase of action potential during which the potential membrane may be more negative than the potential of rest. This phase of potential action is called undershoot or post-supraluminal post-suprareaction. In Figure 1.4, undershoots of action potentials do not become more negative than the potential of rest because they are riding on a constant depolarization stimulus. 1.5 Ion permeabilities Before studying the ion mechanisms of the action of potentials, first you need to understand the ion mechanisms of recreation potential. These two phenomena are closely related. The history of leisure potential dates back to the early 1900s, when Julius Bernstein suggested that the potential of rest (Vm) was equal to potassium equilibrium potential (EK). Where the key to understanding the potential of rest is the fact that the ions are distributed unevenly on the inside and outside of the cells, and that the cell membranes are selectively permeable for ions. CK is especially important for recreation. The membrane is very permeable to the C.K.A. In addition, the inner part of the cell has a high concentration of CK (K) and the outside of the cell has a low concentration of CK (C.C.E.). Thus, the CK will naturally move by diffusion from a region of high concentration to a low concentration area. Consequently, the positive ions of the CK, leaving the inner surface of the membrane, leave behind some negatively charged ions. This negative charge attracts a positive charge of ion 3D, which goes away and tends to pull it back. Thus, there will be an electrical force directed inward, which will usually balance the diffuse force directed outward. Eventually, a balance will be established; the force of concentration, moved by the C.P., balances the electrical force by holding it. The potential with which this balance is achieved is called the potential of the Nernst equilibrium. An experiment to test Bernstein's hypothesis that membrane potential is equal to the potential of northern equilibrium (i.e. Vm and EK) is illustrated on the left. The concentration of CH outside the cell varied systematically, while the membrane potential was measured. Also shown is the line that is predicted by the Nernst equation. Experimentally measured points are very close to this line. In addition, due to the logarithmic relationship in the Nernst equation, a change in the concentration of CK is 10 times the potential change of 60 mV. Note, however, that there are some variations in the picture to the left of what is predicted by the Nernst equation. Thus, it is impossible to conclude that Vm and EK. Such deviations indicate that the other ion is also involved in building the potential of recreation. This ion is Naz. The high concentration of Naz outside the cell and the relatively low concentration inside the cell leads to a chemical (diffuse) driving force for the Naz tributary. There is also an electrical driving force because the inside of the cell is negative and this negative attracts positive sodium ions. Consequently, if the cell has a small sodium permeability, Naz will move through the membrane and the membrane potential will be more depolarized than might be expected from the potential equilibrium of the CK. 1.6 Goldman-Hodgkin and Katz Equation (GHK) When the membrane is permeable to two different ions, the Ernst equation can no longer be used to accurately determine the membrane potential. However, you can apply the GHK equation. This equation describes the potential through the membrane, which is permeable to both Naz and CK. Note α is the ratio of Na permeability (PNa) to PK permeability. Note also that if the permeability of the membrane to Naz is 0, the alpha in GHK is 0, and the equation Goldman-Hodgkin-Katz is reduced to the equilibrium potential of Ernst for KK. If the permeability of the membrane to Naz is very high and potassium permeability is very low, the terms Na become a large, dominant equation compared to the terms KK, and the GHK equation comes down to Nernst's equilibrium potential for Na. If the GHK equation applies to the same data in figure 1.5, it fits much better. The alpha value needed to get this good fit was 0.01. This means that the permeability of CK potassium is 100 times greater than the permeability of Naz. Thus, the potential of rest is not only due to the fact that there is a high permeability of the 3D. There is also a slight permeability of Naz, which tends to make the membrane potential a little more positive than it would be if the membrane was permeable only to CK. 1.7 Membrane Potential Laboratory Click here to go to the interactive laboratory Membrane Potential to experiment with the effects of changes in the external or internal concentration of potassium ions and membrane permeability of sodium and potassium ions. Forecasts are made using the equations of Ernst and Goldman, Hodgkin, Katz. Membrane Potential Laboratory Check Your Knowledge If the nervous membrane suddenly became equally permeable as Naz and CH, the membrane potential will be: A. Do not change B. Approach to the new equilibrium potential of CK C. Approach to the new equilibrium potential Na D. Approach to a value of about 0 mV E. Approach constant value of about 55 mV if the nervous membrane suddenly became equally permeable as Naz and CH, the membrane potential will be: A. Do not change B. 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