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Immediate plasticity of identifiable synapses in the land snails Helix lucorum

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Abstract. The data presented concern synaptic plasticity arising during neuronal response to a single sensory stimulus. The plasticity was studied in identifiable synapses between sensory and command neurones of Helix lucorum using simultaneous intracellular recording. A brief mechanosensory stimulation evoked a train of spikes in an identifiable visceral sensory neurone. Interspike intervals within the train changed from short (tens ms) to long (s). Each spike elicited an elementary EPSP in an identifiable command neurone. The amplitude of elementary EPSPs varied during a train of action potentials. Initial high frequency depression was followed by posttetanic potentiation and subsequent low frequency depression. The result of integration of the three plastic processes has been named immediate plasticity. It has been shown that a compound EPSP elicited in a postsynaptic command neurone by a single sensory stimulus depends on the immediate plastic changes of elementary EPSPs.

Key words: identifiable neurone, identifiable synapse, elementary EPSP, compound EPSP, immediate plasticity, synaptic depression, posttetanic potentiation

INTRODUCTION

Plasticity of synapses presents a background for learning and memory (Eccles 1964, 1993). Plasticity depends on sequence of stimuli. Sensory stimuli are usually used to test plastic modifications at both behavioral and neuronal levels. The test stimuli for a single synapse are single presynaptic action potentials that evoke elementary postsynaptic potentials in follower cells (Kandel 1976). A train of action potentials is a typical response of neurones to a sensory stimulus. We have suggested that each spike within a train evoked in a presynaptic neurone by a sensory stimulus produces in a follower cell a change of synaptic efficacy. We have named these changes immediate plasticity (Palikhova and Sokolov 1997). We have also suggested that a compound synaptic response of a postsynaptic cell to a single sensory stimuli depends on the immediate plasticity of elementary postsynaptic potentials as well as on their space and time summation. The goal of the present research was to test immediate plasticity at the synapses between identified neurones in the land snail Helix lucorum.

Molluscs, and snails in particular, are used as experimental model to study the mechanisms of plasticity at the behavioural, neuronal and synaptic levels (Tauc 1966, Kerkut 1969, Sakharov and Shalanki 1967, Sakharov 1974, 1994, Bullock and Basar 1988). Molluscs present a possibility to record electrical activity simultaneously from both pre- and postsynaptic neurones that can be activated by sensory stimulation (Kandel 1976, Byrn 1987, Sokolov 1991). Such a possibility is a necessary condition to study immediate plasticity. Synaptically connected identifiable neurones have been found in the central nervous system of the land snail Helix lucorum (Logunov and Balaban 1978)). It has been shown that some of the identified presynaptic cells are interceptive sensory neurones (Palikhova and Arakelov 1990, Sokolov 1991). The postsynaptic cells are the command neurones that central the snail's escape behaviour (Sokolov 1977, Balaban 1979). It has been shown that elementary excitatory postsynaptic potentials (eEPSPs) elicied at the command neurones by the presynaptic spikes consist of monosynaptic and polysynaptic components (Palikhova et al. 1994). The monosynaptic components have been proposed to be cholinergic (Ter-Markaryan et al. 1991) and consist of several subcomponents (Marakujeva et al. 1992).

Synaptic connections repeatedly identified in various preparations are termed identifiable synapses (Sokolov and Logunov 1985). The precondition to such regular identification is based on identifiable neurones injected by dyes (Arakelov and Sakharova 1982). Synapses between sensory neurones representing internal organs and command neurones of defensive behaviour have been anatomically identified in the land snail Helix (Arakelov et al. 1991, Marakueva et al. 1992). Parallel injections of different dyes into a sensory neurone representing viscera of the animal (neuron LPa7) and the defensive command neurone (LPa3) have shown that the sensory neurone builds up 8-9 buttons on the dendrites of the command neurone (Marakueva et al. 1992).

The synapses between sensory cells and command neurones display several types of plastic changes (Logunov 1984, Sokolov and Palikhova 1991, Sokolov 1991). This paper refers to a plasticity arising immediately after single sensory stimulation of internal organs or direct electrical intracellular stimulation of an identified sensory neurone. To test the immediate plasticity, double intracellular recordings from sensory and command neurones in a semi-intact preparation were made during sensory stimulation of the internal organs and during intracellular stimulation of a sensory neurone. It could be shown that immediate plasticity revealed by a change of elementary excitatory postsynaptic potential (eEPSP) is the result of three types of processes: (1) initial short-term depression of eEPSPs evoked by a high frequency train of action potentials, (2) following posttetanic potentiation of eEPSPs evident by a decrease of spiking frequency and (3) subsequent low-frequency depression or habituation of eEPSPs.

METHODS

Preparation

Adult land snails Helix lucorum from a Crimea population were used. Experiments were performed on preparations consisting of central ganglia, mantle collar and viscera (Palikhova and Arakelov 1990) and on modified "dissected foot" preparations (Shekhter 1980, Bravarenko et al. 1982, Arakelov et al. 1991). The preparations were placed in a bath containing extracellular solution (in mM): 80 NaCl, 4 KCl, 8 $CaCl_2$, 5 $MgCl_2$, 4 Tris-HCl (pH 7.8). Low-temperature (8-12°C) anaesthesia was used during operations. Recordings were performed at room (20-22°C) temperature.

Recording

Intracellular, somatic whole-cell current-clamp recordings were obtained simultaneously from the identified presynaptic and postsynaptic neurones. Identification of the command and the sensory neurones was based on morphological and physiological criteria (Arakelov et al. 1991, Ierusalimski et al. 1994, Palikhova et al. 1994). Intracellular microelectrodes filled with 2.5 M KCl had resistance of 10-20 MΩ for pre- and 1-5 MΩ for postsynaptic neurones. The large soma size of command neurones, 200-300 μm, allowed us to use low-resistance pipettes to record low-amplitude postsynaptic potentials. Signals obtained from sensory and command neurones were amplified with MEZ-8201 (Nihon Kohden, Japan) and MS-03 (Minsk, Belorus) amplifiers. Data were stored on computer by an analog to digital converter and program DS (Digiscope, Moscow) for monitoring, recording and subsequent analysis.

Stimulation

Intracellular current injection and tactile stimulation of the visceral organs were used to elicit spikes in the sensory neurones. Currents were injected into a cell through the recording microelectrode by means of a bridge circuit. Temporal parameters of the injected current depended on the experimental task. For rhythmic stimulation within a range of frequencies from 0.005 to 10 Hz short (5-50 ms) current pulses (1-10 nA) were used. Direct current injections into the sensory neurone had been used to trigger trains of presynaptic spikes that simulated trains of spikes elicited by sensory stimuli. Calibrated hairs (0.1-0.2 mm 0.4-1.5 G) connected with a solenoid and operated by an electrostimulator MSE-3R (Nihon Kohden, Japan) were used for sensory tactile stimulation.

Data from presynaptic sensory LPa7 and LPa9 and postsynaptic command neurones LPa3 and RPa3 stu-

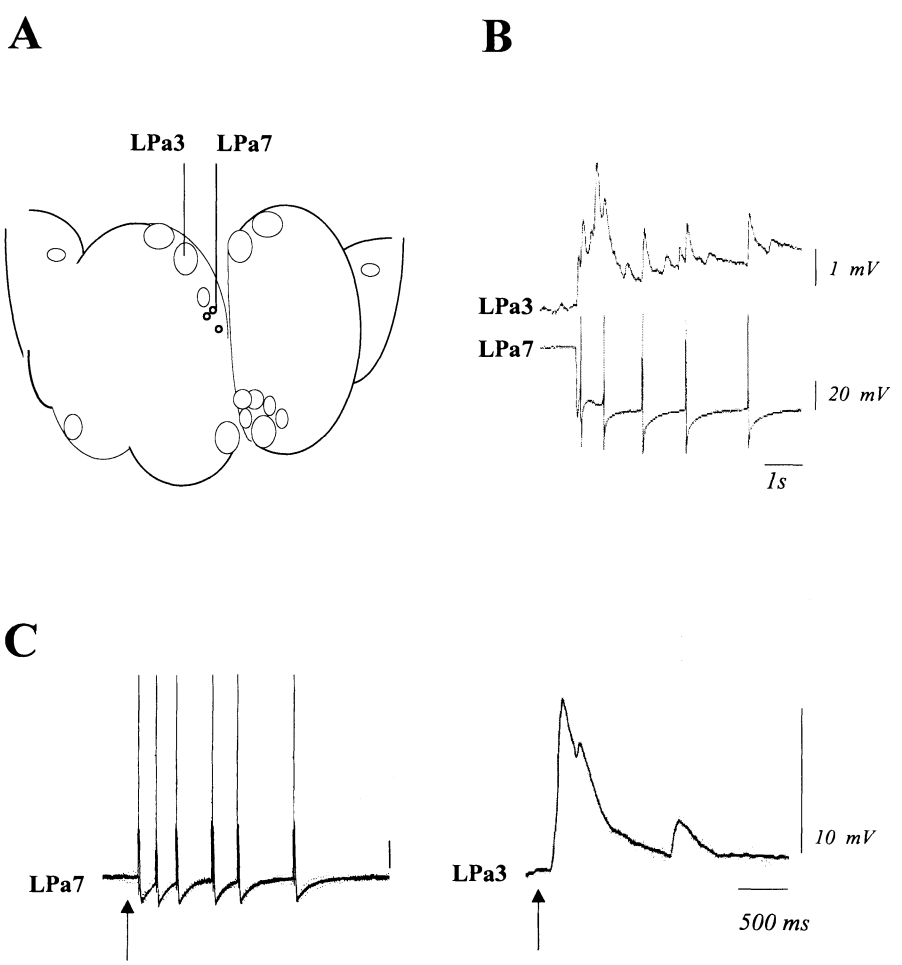

Fig. 1. Monosynaptically connected identifiable sensory (LPa7) and command (LPa3) neurones are marked on a scheme of parietal complex ganglia of Helix lucorum (A) that is a simplification of the map (Ierusalimski et al. 1992, 1994) based on the classical one (Sakharov and Shalanki 1969, Sakharov 1974). Detailed information on the localization of cell bodies of the identified presynaptic neurones can be found in (Arakelov et al. 1991, Palikhova et al. 1994). B, elementary EPSPs evoked in the command neurone by presynaptic action potentials elicited by a micropipette penetration into a presynaptic neurone. C, typical burst of spikes elicited by brief sensory stimulation (arrows) in identifiable sensory neurone and typical compound EPSP evoked in LPa3 command neurone by the sensory stimulus.

died systematically were obtained in about 50 experiments.

RESULTS

Elementary and compound postsynaptic potentials

Action potentials (APs) generated in an identifiable sensory neurone of a snail evoke elementary excitatory postsynaptic potentials (eEPSPs) in parietal command neurones (Fig.1B). A brief tactile stimulation of the mechanosensory surface of an animal results in a burst of action potentials (APs) in an identifiable sensory neurone and evokes a compound EPSP (cEPSP) in a command neurone (Fig. 1C). Mechanosensory receptive fields of the sensory and command neurons were studied to appreciate the contribution of single eEPSPs to cEPSP.

Receptive field of an identifiable sensory neurone

Local tactile stimulation of different areas of the skin and the internal organs demonstrated a "point-like" excitatory area of the sensory neurone surrounded by an inhibitory zone (Fig. 2A). The APs evoked by stimulation of the excitatory area were not preceded by EPSPs (Fig. 2B) indicating that they are arising in the dendrites of T- shaped sensory cell by-passing its cell body. Axonal spikes (A-spikes) were recorded in the sensory neuron when APs did not activate a neuronal soma. Responses evoked in the areas surrounding a point-like zone in turn were characterized by inhibitory postsynaptic potentials suggesting synaptic lateral inhibition be-

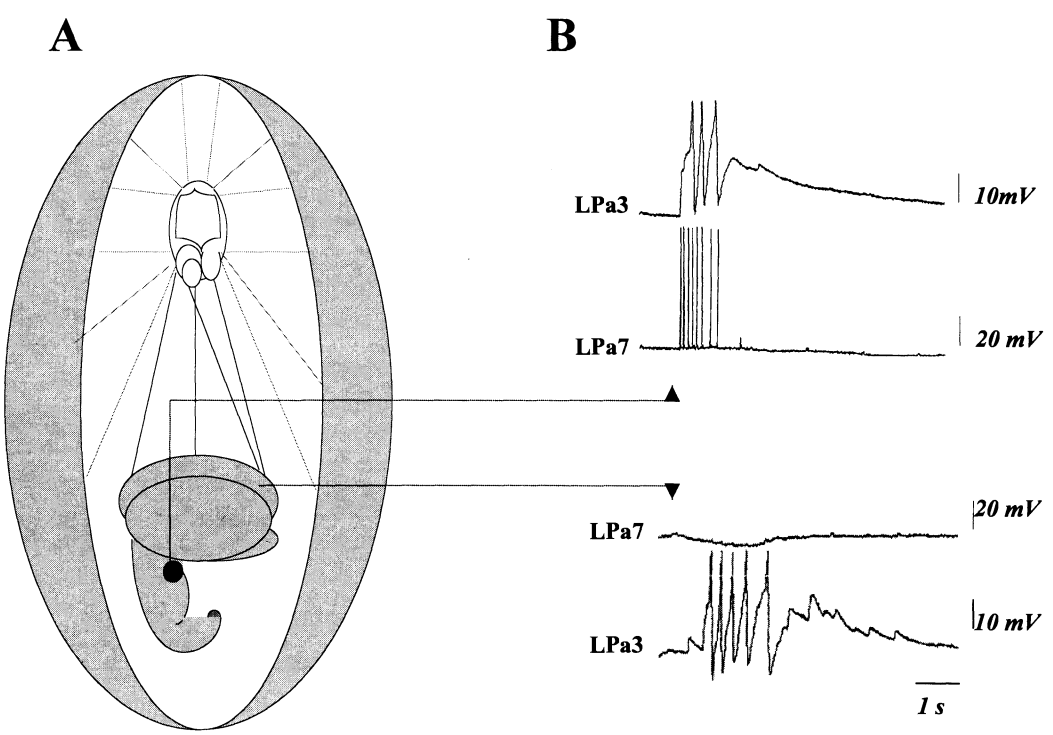

Fig. 2. Mechanosensory receptive fields of the sensory and the command neurones. A, a scheme of a semi-intact snail preparation (Sokolov 1991, Balaban and Zakharov 1992). Mechanoreceptive field of LPa7 neurone consists of both excitatory and inhibitory areas. The excitatory area of the LPa7 receptive field is marked by black in viscera on the scheme. The giant excitatory mechanoreceptive field of LPa3 command neurone is marked by gray. The inhibitory area of the sensory neurone receptive field coincides with the excitatory receptive field of the command neurone. B, simultaneous recordings of responses of the sensory neurone and the command neurones to tactile stimulation of two different areas of mechanoreceptive surface of an animal. The stimulation of viscera evokes in LPa7 neuron APs without preceding membrane potential change. Tactile stimulation of the mantel collar results in hyperpolarisation of the sensory neurone. Both stimuli evoke compound EPSP and AP generation in the command neuron (APs are truncated because of high amplification).

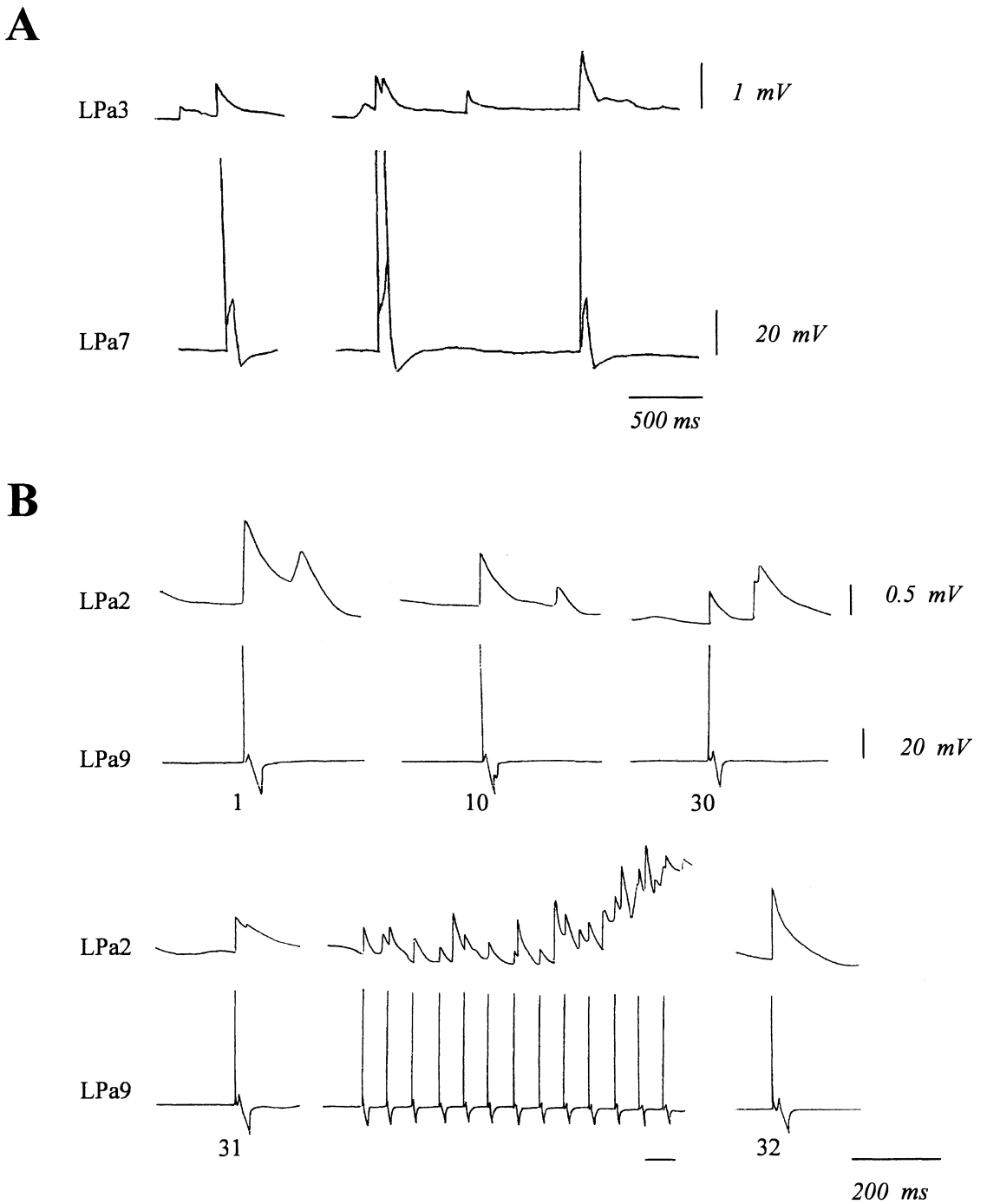

Fig. 3. Plasticity of synapses between sensory and command neurones. A, doubled presynaptic APs presented during series of low-frequency stimulation of the presynaptic sensory neurone (0.1 Hz, 100 ms, 2 nA) evoke an increase of eEPSP amplitude following single AP. B, repeated stimulation of the sensory neurone by short current pulses (0.03 Hz, 50 ms, 10 nA) results in low-frequency depression of eEPSPs in the command neurone. High-frequency (5 Hz) burst of presynaptic APs presented during the low-frequency series elicits high-frequency depression of eEPSPs during and posttetanic potentiation after the burst. Shift of membrane potential of the command neurone during high-frequency stimulation of the sensory neurone is a result of summation of the late polysynaptic components of command neurone responses (Palikhova et al. 1994) which have their own dynamics during repeated stimulation of the sensory neurone.

tween sensory neurones. Repeated sensory stimulation of the excitatory focus of the receptive field revealed no plastic changes of excitatory responses (Palikhova and Arakelov 1990, Sokolov 1991).

Receptive field of the command neurone

While the receptive field of the sensory neurone has a local excitatory area, any stimulation of skin or internal organs produced in the command neurone EPSPs supplemented occasionally by action potentials (Fig. 2B). In contrast to the stable responses of the sensory neurones the command neurone revealed EPSP and AP habituation. The habituation was selective with respect to stimulus location. This suggests that different loci of the skin surface and the internal organs are represented by parallel channels served by single sensory neurones with local excitatory areas (Shekhter 1980, Bravarenko et al. 1982, Shekhter and Arakelov 1985).

Responses of the command neurone to single presynaptic APs

Properties of a sensory neurone as an informational channel signaling to the command neurone events occurring in a local area of the internal organs were studied by electric stimulation of its cell body. Short (5-50 ms) depolarizing pulses evoked single action potentials in the sensory neurone which triggered eEPSPs in the command neurone. Repeated stimulation of the sensory neurone with frequencies in the range of 0,01 Hz to 10 Hz was followed by eEPSPs with gradual decreasing amplitudes, showing plastic properties of the identifiable synapse (Fig. 3).

Responses of the command neurone to a train of presynaptic APs

A brief sensory stimulus evoked in a sensory neurone a train of action potentials. Duration of the spike trains was similar to the duration of the compound EPSPs recorded simultaneously in a command neurone (Fig. 2B). To simulate the results of a local sensory stimulation, trains of APs were triggered in sensory neurones by depolarizing pulses. The simplest train is a sequence of two action potentials. If intervals between action potentials were in the range of 50-200 ms, the eEPSP to the second AP was significantly reduced demonstrating immediate depression. If, however, the doubled action potentials were followed after 500 ms - 10 s with another AP, the amplitude of the eEPSP evoked by this AP was enhanced with respect to the initial value suggesting immediate potentiation even after doublet of APs (Fig. 3A).

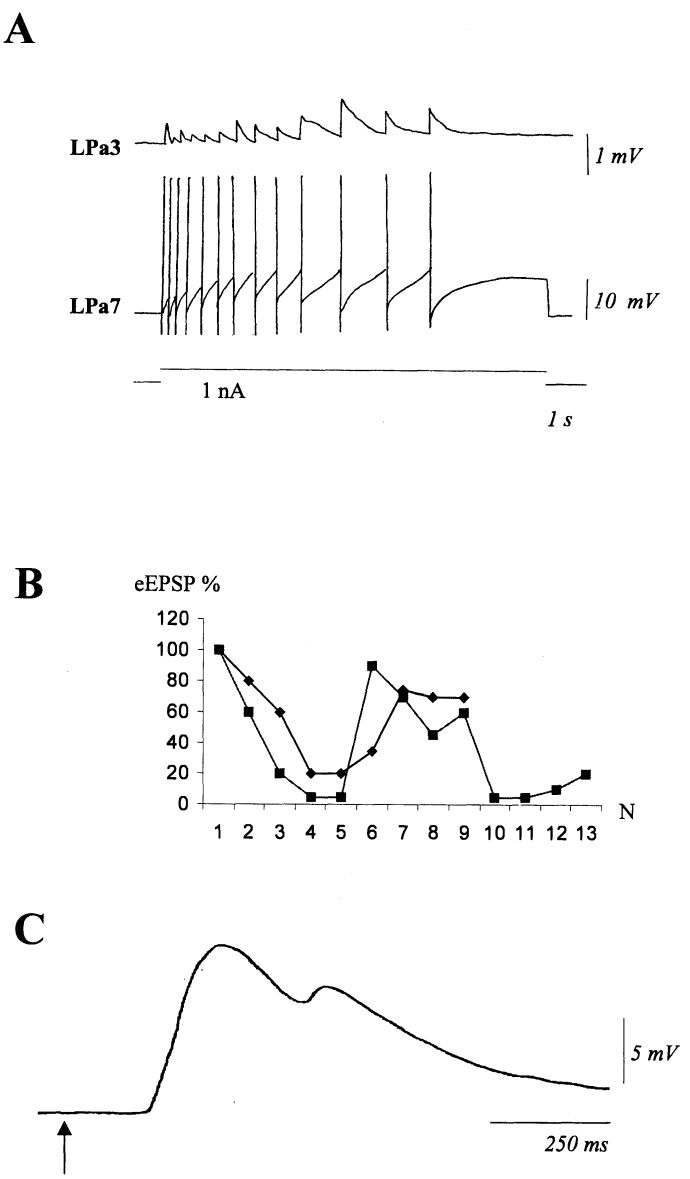

Fig. 4. Dynamics of eEPSPs evoked by APs from irregular trains. A, dynamics of eEPSPs amplitude during a train of presynaptic APs elicited by intracellular injection of direct current (1nA). B, average dynamics of eEPSPs in a command neurone evoked by presynaptic APs elicited by single sensory stimuli (line marked with large squares, n = 6) and during stimulation of a presynaptic sensory neurone by direct current injection (line marked with small squares, n = 6). C, average cEPSP evoked in LPa3 command neurone by sensory stimulation.

An increase in the number of APs in a train evokes a more pronounced potentiation and prolongs its effect (Fig. 3B). For example, a train of ten presynaptic APs evoked an increase of the eEPSP amplitude that could be observed several minutes after the high-frequency stimulation. The potentiation in both cases can be termed "posttetanic potentiation " (Eccles 1964, Palikhova and Sokolov 1994).

Trains of APs elicited in an identifiable sensory neurone by brief sensory stimuli consisted of 5-10 spikes. Interspike intervals within the trains varied from 50 ms at the beginning to 500 ms - 1s at the end. It was possible in several experiments to distinguish eEPSPs from cEPSPs elicited by the sensory stimuli. The experiments have shown that the amplitude of eEPSPs decreased at the beginning and increased at the tail of the compound responses of the command neurone. Trains of APs with patterns similar to that elicited by sensory stimuli could be simulated by current injected into the soma of an identified sensory neurone (Fig. 4A). The amplitudes of eEPSPs evoked by the direct current injection changed in ways similar to the eEPSPs evoked by sensory stimulation (Fig. 4B). A diagram of eEPSP amplitude dynamics during a train of presynaptic spikes resembled that of the shapes of the typical cEPSP elicited in a command neurone by brief sensory stimulation (Fig. 4C).

DISCUSSION

A sensory neurone representing a local area of the receptive surface of internal organs constitutes one of multiple parallel informational channels converging on a defensive command neurone (Sokolov 1977). Sensory neurones demonstrate remarkable response stability while their synapses on a command neurone are highly plastic. During a train of action potentials elicited in the sensory neurones by brief sensory stimulation an immediate depression of synaptic transmission to the command neurones is evident. Immediate depression is followed by an immediate potentiation.

High-frequency depression and potentiation are both presynaptic phenomena (Eccles 1964, Kandel 1976). We suggest the same for the immediate depression and potentiation. Our interpretation of the data obtained in the identifiable synapse of the snail is similar to that given by John Eccles for curarized neuromuscular connections and synapses on motoneurones of vertebrates (Eccles 1964). The differences concern the frequencies of presynaptic stimulation used to obtain depression or potentiation of the postsynaptic responses. We used in our experiments the frequencies of presynaptic spikes that were recorded in responses to natural, mechanosensory stimulation. In this range of frequencies the dynamics of postsynaptic responses depend on the pattern of presynaptic spikes.

It is generally accepted that decrease of transmitter release is the main reason for high-frequency depression (Eccles 1964). Every presynaptic spike decreases number of vesicles connected with presynaptic membrane. Depression depends on the relationship between number of expressed vesicles and number of vesicles prepared to release. Recovery time depends on the intensity of previous expressions. The intensity of expression depends on the probability of expression determined by presynaptic calcium concentration (Llinas 1994). The mechanism of immediate potentiation is also suggested to be of presynaptic origin. The general point of view now is that transmitter release increases with the broadening of presynaptic spikes (Kandel and Schwartz 1982, Klein et al. 1982, 1986, Hochner et al. 1986).

The same mechanism has been suggested for plastic changes in synaptic connections of the command neurones of Helix (Zakharov et al. 1995). The second messenger pathways are discussed as a mechanism of synaptic plasticity (Byrn et al.1993, Kostuk et al. 1998). Thus the same event, a presynaptic spike, triggers both presynaptic depression and potentiation. Plasticity of a synapse depends on a ratio of these processes that differ in time course.

The dynamics of transmitter release is highly specific characteristics of identified synapses. The probability of transmitter release varies not only in different cells but also at different terminals of the same neurone and depends on its postsynaptic targets (Davis et al. 1994). In different cells the probability of expression varies from very low as at the synapses on pyramidal neurones in the cortex (Eccles 1993) to very high as in noncurarized neuro-muscular junctions (Eccles 1964) and squid giant synapses (Llinas 1994). The identifiable synapses in snails are in the middle of the list.

The action potentials generated in a sensory neurone with intervals in the range 1-100 s produced a gradual decrease of eEPSPs amplitudes that might be related to the postsynaptic mechanism of desensitization of receptors. The postsynaptic nature of low-frequency depression is suggested by data obtained in experiments on isolated cell bodies of the command neurones (Grechenko 1985)

and by experiments showing differential plasticity of eEPSP subcomponents (Marakueva et al. 1992).

Thus, complete excitation of the command neurone to sensory input is the result of the integration of three plastic processes which are high-frequency depression, posttetanic potentiation and low-frequency depression, evoked during a train of action potentials arriving from a sensory neurone in response to a single local sensory stimulus. These plastic changes occurring during neuronal response to a sensory stimulation can be termed immediate plasticity. Immediate plasticity contributes to the shape of the compound postsynaptic response of a command neurone. This is suggested by the fact that usually two peaks were observed in cEPSPs elicited in a command neurone by sensory stimulation reflecting an initial response to high-frequency stimulation that is followed by depression and following posttetanic potentiation of eEPSPs. During repeated sensory stimulation posttetanic potentiation is accompanied by habituation (low frequency depression) of cEPSPs in a command neurone.

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