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Tactile response adaptation to whisker stimulation in the lemniscal somatosensory pathway of rats

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ABSTRACT

Response adaptation is associated with attenuation of neural responses as the result of different mechanisms. However, the main function of adaptation may be to enhance the flow of relevant information transmission in sensory pathways. To study tactile response adaptation in the somatosensory pathway, unit recordings were performed in the principal trigeminal nucleus, ventro postero-medial thalamic nucleus and barrel cortex by means of tungsten microelectrodes in urethane anesthetized rats. Tactile stimuli consisted in 20 ms duration whisker deflections at different frequencies (0.5–10 Hz). Presumably pyramidal cortical neurons showed response adaptation at frequencies >2 Hz while putative inhibitory cortical neurons did not show response adaptation at 0.5, 5 or 10 Hz. Inhibitory activity was increased by muscimol application into the cortex (8 mM, 0.1 μl); in this condition cortical adaptation was not affected, suggesting that adaptation was not due to an increase of inhibitory mechanisms. Adaptation was also observed in subcortical structures although the response attenuation was lesser than in the barrel cortex. Adaptation remained in subcortical structures after reversible cortical inactivation by cooling the barrel cortex. Acetylcholine application (10 μM; 0.1 μl) into the barrel cortex reduced response adaptation through the activation of muscarinic receptors because the effect was blocked by intraperitoneal injection of atropine (1 mg/kg), suggesting that adaptation may change according to the cortical Ach level. Results indicate that response adaptation increases along the somatosensory pathway probably to alter the sensitivity of neurons in order to encode sensory stimuli more efficiently and to enhance the detectability of rare stimuli.

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1. Introduction

Adaptation is a ubiquitous property within different sensory pathways of the brain (Ahissar et al., 2000; Higley and Contreras, 2006; Maravall et al., 2007). Although associated with an attenuation of neural responses as the result of different mechanisms, adaptation is also thought to enhance the flow of relevant information transmission in sensory pathways in complex environments.

In the somatosensory system, rats use rapid backward and forward whisker movements during tactile exploration to sample the physical environment around them (Brecht et al.,

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1997; Carvell and Simons, 1990; Welker et al., 1992). In this sensory system adaptation is particularly strong in the neocortex (Chung et al., 2002) but is also present in the thalamus and trigeminal nuclei (Castro-Alamancos, 2009). Robust adaptation is observed in the barrels and septa of layer IV of the somatosensory cortex (Ahissar et al., 2000, 2001; Castro-Alamancos, 2002b; Chung et al., 2002; Simons, 1978). Also, repetitive whisker deflections above 2 Hz produce strong adaptation of tactile responses in layer 2/3 neurons and deflections above 1 Hz in layer 5/6 neurons of urethane anesthetized rats (Ahissar et al., 2000; Chung et al., 2002; Sheth et al., 1998). It has been suggested that adaptation is a processes to enhance sensory coding and perception of repetitive stimuli (Adorjan et al., 1999; Fairhall et al., 2001; Kohn and Whitsel, 2002). The frequencies of whisker motion displayed during rest (<1 Hz) and whisking (4–12 Hz) may optimize the vibrissa processing system for the detection or discrimination of stimulus features, respectively (Moore et al., 1999; Nicolelis and Fanselow, 2002). During rest, general alertness to incoming stimuli is crucial, whereas during whisking, the ability to make fine and rapid discriminations between stimuli is potentially more important.

Cerebral cortex and hippocampus are largely innervated by cholinergic projections from the basal forebrain (Mesulam et al., 1983). It has been indicated that cortical acetylcholine (Ach) augments the processing of sensory information, enhancing the responsiveness of cortical neurons by activation muscarinic and nicotinic receptors (see for recent reviewers (Hasselmo and Sarter, 2011; Levin et al., 2006b; Pauli and O'Reilly, 2008; Sarter et al., 2014)). Accordingly, increases in cortical Ach are observed upon presentation of relevant stimuli that presumably increase the level of arousal and/or attention (Alenda and Nuñez, 2007; Dalley et al., 2001; Himmelheber et al., 2000; Lendvai et al., 2000; Nuñez et al., 2012). The effect of Ach varies greatly depending on whether it binds to nicotinic or muscarinic receptors. Data from in vitro preparation have demonstrated that nicotinic receptors selectively enhance afferent thalamocortical inputs (Gil et al., 1997; Gioanni et al., 1999) while muscarinic cholinergic agonists reduced synaptic transmission of corticocortical afferents (Vidal and Changeux, 1993). Accordingly, cortical Ach could switch between a predominant influence of external, thalamocortical inputs to a predominant influence of internal, corticocortical inputs and participate in regulating attention, learning, and memory processes (e.g. Giocomo and Hasselmo, 2007; Levin et al., 2006a, 2006b). Arousal, attentional or exploratory behaviors are associated with pronounced adaptation changes in thalamocortical circuits (Castro-Alamancos, 2004). In anesthetized rats, whisker stimulation above 2 Hz induces a frequency-dependent depression of thalamic neurons. However, during activated states ventro postero-medial thalamic (VPM) cells can follow whisker stimulation efficiently at frequencies of up to 40 Hz, and even 100 Hz (see also Castro-Alamancos, 2002a). Thus, cortical response adaptation may be altered by the level of cortical Ach. In the somatosensory cortex Ach increases the responses to a whisker stimulus in anesthetized rats mainly by activation of muscarinic receptors (Donoghue and Carroll, 1987; Lamour et al., 1986). The cellular and synaptic mechanisms contributing to sensory adaptation in the cortex are only partially understood. Consequently, we have examined responses to repetitive tactile stimuli at frequencies that mimic natural whisking conditions. We performed unit recordings in the somatosensory pathway of anesthetized rats and measured response adaptation in the principal trigeminal (Pr5) nucleus, ventro postero-medial thalamic (VPM) nucleus and barrel cortex.

2. Results

2.1. *Response adaptation in the barrel cortex*

Cortical cells were recorded in the barrel cortex at depths of 200–600 μm ($n=139$), corresponding to layers 2/3 or at depths of 800–1500 μm ($n=127$), presumably corresponding to layer 5/6 (Fig. 1A). Neurons were classified into two types according to their spontaneous firing rate spike. Type 1 cells ($n=266$; 95%) had a low spontaneous activity (<2 spikes/s; mean 0.5 ± 0.2 spikes/s) while type 2 cells ($n=15$; 5%) displayed a higher spontaneous discharge rate (>10 spikes/s; mean 16.5 ± 3.7 spikes/s; $p<0.001$). Moreover, type 1 cells had a mean spike duration of 0.7 ± 0.3 ms (negative component of the spike) while type 2 neurons had a shorter spike duration (0.4 ± 0.3 ms; negative component of the spike; $p<0.001$; Fig. 1B; insets in C and D shows representative examples).

Type 1 neurons in layer 2/3 responded to stimulation of one or two whiskers. The mean response of the principal whisker (with the highest spike response) was 0.9 ± 0.1 spike/stimulus when they were stimulated at 0.5 Hz; the mean latency was 14 ± 2 ms ($n=139$; Fig. 1C). Similar tactile responses were observed in layer 5/6 neurons in comparison with layer 2/3 neurons (0.8 ± 0.1 spike/stimulus and 15 ± 2 ms latency; $n=127$; $p=0.77$ and $p=0.24$). The low spontaneous firing rate and the reduced receptive field (RF; one-two whiskers) provide strong support to the notion that recordings were obtained from putative pyramidal cells, as has been previously reported (de Kock et al., 2007; de Kock and Sakmann, 2008; Manns et al., 2004). Neurons included in our study are probably located in the barrel because these neurons showed small RFs and a short response latency. Moreover, the response efficacy of our neuronal population was similar to previously reported data for barrel neurons and efficacy was distant from neurons recorded in the septa (Melzer et al., 2006).

We did not find differences among type 2 neurons from layer 2/3 or layer 5/6. Thus, we pooled together the data for the following studies. Type 2 neurons in both layer 2/3 and layer 5/6 showed a mean response of 3.3 ± 0.7 spike/stimulus when they were stimulated at 0.5 Hz; the mean latency was 16 ± 4 ms ($n=15$; Fig. 1D). While type 1 neurons responded in a short time window after whisker deflection (between 10 and30 ms), type 2 neuronal responses could last up to 50 ms after the stimulus onset (Fig. 1C and D). These firing properties suggest that they could be local interneurons (see for review, Markram et al., 2004).

Responses to periodic tactile stimuli were examined in 139, layer 2/3 type 1 cortical neurons. These neurons exhibited a gradual decrease in responsiveness over the 0.5- to 10-

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