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Short communication

Dynamic properties of sensory stimulation evoked responses in mouse cerebellar granule cell layer and molecular layer

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HIGHLIGHTS

- The cerebellar granule cell layer expresses high-frequency and -fidelity properties in response to sensory stimulation.
- The high frequency sensory information coming from granule cell layer is cut-off in molecular layer.
- The molecular layer interneuron network acts as a low-pass filter in cerebellar cortex during the sensory information processing.

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ABSTRACT

Sensory information coming from climbing fiber and mossy fiber-granule cell pathways, generates motor-related outputs according to internal rules of integration and computation in the cerebellar cortex. However, the dynamic properties of sensory information processing in mouse cerebellar cortex are less understood. Here, we studied the dynamic properties of sensory stimulation-evoked responses in the cerebellar granule cell layer (GCL) and molecular layer (ML) by electrophysiological recordings method. Our data showed that air-puff stimulation (5–10 ms in duration) of the ipsilateral whisker pad evoked single-peak responses in the GCL and ML; whereas a duration of stimulation ≥30 ms in GCL and ≥60 ms in ML, evoked double-peak responses that corresponded with stimulation-on and -off responses via mossy fiber pathway. The highest frequency of stimulation train for evoking GCL responses was 33 Hz. In contrast, the highest frequency of stimulation train for evoking ML responses was 4 Hz. These results indicate that the cerebellar granule cells transfer the high-fidelity sensory information from mossy fibers, which is cut-off by molecular layer interneurons (MLIs). Our results suggest that the MLIs network acts as a low-pass filter during the processing of high-frequency sensory information.

1. Introduction

The cerebellum includes three cortical layers, which involves five main types of neurons organized in a lattice-like structure that receives two distinctly different types of excitatory afferents: the mossy fibers and the climbing fibers. Cerebellar granule cells receive information from mossy fiber inputs, and convey the information to PCs via parallel fibers. Granule cells exhibit a low frequency of spontaneous firing under in vivo conditions, but are very sensitive to sensory stimulation [1–4]. Air-puff stimulation of the vibrissae evokes high-frequency excitatory responses in granule cells, with a maximal instantaneous frequency as high as 250 Hz [2]. Sensory stimulation evoked bursts of granule cells consisting of tens of spikes, at instantaneous frequencies over 800 Hz, in both unanesthetized rabbits and mice [4]. Therefore, granule cells are presumed to serve as a high-pass spatiotemporal filter, through which information transfers from mossy fibers to PCs [5,6]. Our previous study showed that sensory stimulation evoked excitatory field potentials which expressed stimulation-on and stimulation-off information in the mouse cerebellar GCL, suggesting that granule cells expressed high frequency property

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in response to sensory stimulation [7]. However, we found that facial stimulation of trigeminal afferents primary induced GABAergic inhibition to Purkinje cells but evoked fast spike firing in MLIs of the cerebellar cortex Crus II, indicated that cerebellar MLIs play a critical role during the sensory information processing in cerebellar cortex cerebellar [8–10]. The structure of the network of inhibitory interneurons in the mammalian cerebellar cortex has been described in great detail [11]. The MLIs include basket and stellate cells, which receive excitatory input from parallel fibers and inhibitory input from other interneurons [11–13]. Stellate cells provide dendritic inhibition, which is predicted to specifically counterbalance the parallel fiber excitation in local regions of the PC dendrites [14,15], resulting in less direct effects on the spiking output of PCs [16]. Basket cells offer somatic inhibition, which is powerful and rapid [17], and results in direct effects on the spiking output of PCs by inhibition of the soma and initial segment of PCs [18,19]. Although the sensory information transferred by granule cells and modulated in the ML, the dynamic properties of sensory information processing in cerebellar GCL and ML are less well understood. Therefore, here we studied the dynamic characterization of sensory stimulation-evoked responses in the GCL and ML by electrophysiological recording method.

2. Materials and methods

2.1. Anesthesia and surgical procedures

Experimental procedures were approved by the Animal Care and Use Committee of Jilin University and were performed in accordance with the animal welfare guidelines of the National Institutes of Health (permit no. SYXK(Ji) 2007-0011). The anesthesia and surgical procedures have been described previously [8]. In brief, 34 adult (6–8-week-old; 15 female, 19 male) ICR mice were anesthetized with urethane (1.3 g/kg body weight, intraperitoneal injection). After a watertight chamber was created, a 1–1.5 mm craniotomy was drilled to expose the cerebellar surface corresponding to Crus II. The brain surface was constantly superfused with oxygenated artificial cerebrospinal fluid (ACSF) (mM: 125 NaCl, 3 KCl, 1 $MgSO_4$, $2CaCl_2$, 1 NaH_2PO_4, 25 $NaHCO_3$, and 10 D-glucose) with a peristaltic pump (Gilson Minipulse 3) at 0.4 ml/min. Rectal temperature was monitored and maintained at 37.0 ± 0.2 °C by body temperature equipment.

2.2. Electrophysiological recordings and sensory stimulation

Local field potential recordings were performed with an axopatch-200B amplifier (Molecular Devices, Foster City, CA). The recording traces were acquired through a digidata 1440 series analog-to-digital interface on a personal computer using Clampex 10.3 software (Molecular Device, Foster City, CA, USA). Recording electrodes were filled with ACSF, with resistances of 3–5 MΩ. Tactile stimulation on the ipsilateral whisker pad was performed by air-puff (10–500 ms, 50–60 psi) through a 12-gauge stainless steel tube connected to a pressurized injection system (Picospritzer® III; Parker Hannifin Co., Pine Brook, NJ). For examine the frequency properties of the sensory stimulation-evoked responses in GCL and ML, we prepared stimulation trains (10-pulse) at 0.25 Hz, 1 Hz, 2 Hz, 4 Hz, 8 Hz, and 33 Hz (10 ms, 50–60 psi).

2.3. Statistical analysis

Electrophysiological data were analyzed using Clampfit 10.3 software. All values are expressed as the mean ± SEM, and differences were evaluated by the student's paired *t*-test or one-way ANOVA using SPSS (Chicago, IL) software. *P* values below 0.05 were considered to indicate a statistically significant difference between experimental groups.

3. Results

3.1. Dynamic properties of facial stimulation-evoked field potentials in the GCL

The minimum duration of facial air-puff stimulation for evoking GCL field potentials was 5 ms (Fig. 1A), which evoked a single-peak response with a mean amplitude of 0.60 ± 0.04 mV (n = 7; Fig. 1A and B). A duration of facial air-puff stimulation of 10 ms evoked a single-peak response with a mean amplitude of 0.64 ± 0.06 mV (n = 7; Fig. 1A and B). When the air-puff stimulus duration was ≥30 ms, a double-peak response was evoked, which corresponded with the stimulation-on response (R_{on}) and

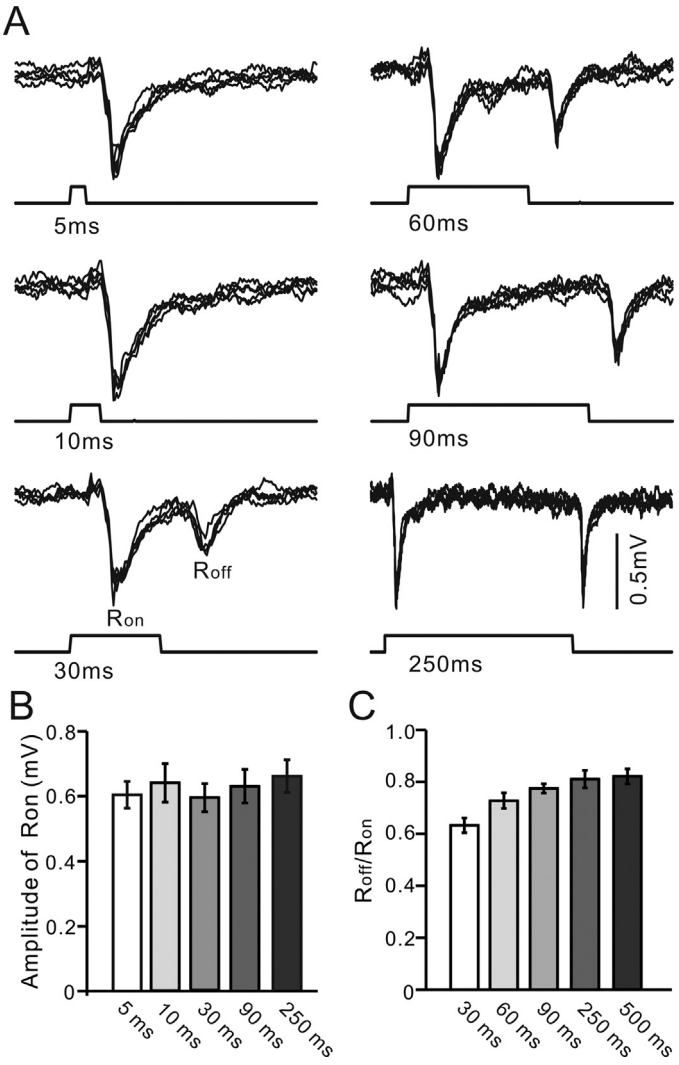

Fig. 1. Properties of the facial stimulation in different durations evoked field potentials in GCL.
(A) Five consecutive field potential recording traces showing the facial stimuli of different durations evoked responses in GCL. The durations of stimuli were 5 ms (upper, left panel), 10 ms (middle, left panel), 30 ms (lower, left panel), 60 ms (upper, right panel), 90 ms (upper, right panel), and 250 ms (upper, right panel). Note that the durations in 5 ms and 10 ms evoked a single peak of response (R_{on}), whereas the longer duration (≥30 ms) evoked double-peak responses (R_{on} and R_{off}). (B) Summary of data (n = 7) showing the relationship between durations of stimuli and the amplitude of R_{on}. (C) Pooled data (n = 7) showing the relationship between durations of stimuli and R_{off}/R_{on} value. Error bars indicate SEM.