Properties of tactile responses of neurons in rat thalamic ventroposterolateral nucleus

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Abstract: Objective To determine whether the convergences of tactile information also occur at thalamic ventroposterolateral nucleus in rats, we investigated the properties of tactile responses of the thalamic ventroposterolateral nucleus in rats. **Methods** Unit responses were recorded extracellularly from thalamic ventroposterolateral nucleus in anesthetized rats. **Results** Among 156 neurons examined, 140 neurons (89.7%) had the single, continual and small receptive fields, and 16 neurons (10.3%) had two discrete receptive fields. Some neurons exhibited different responses to the same intensity stimulation which delivered to different points in their receptive fields. In addition, 4.5% neurons ($n = 7$) responded only to locomotive stimulation but not to a punctiform tactile stimulation. **Conclusion** The majority of neurons in ventroposterolateral nucleus of rats have the spatial, temporal and submodal characteristics of cutaneous receptors, while the minority of neurons exhibit the responses of interaction of different peripheral receptors. Therefore, it is concluded that there are convergences of tactile information at the ventroposterolateral nucleus of rats.

Keywords: thalamus; ventroposterolateral nucleus; tactile response; receptive field; convergence

1 Introduction

Neurons within the dorsal column lemnisco-thalamic pathway have classically been considered to securely preserve the spatial, temporal and submodal characteristics of cutaneous receptors^[1–3]. The reason for the apparent absence of complex interaction of various receptor inputs at thalamic and cortical levels in previous studies was probably due to the lack of controlled mechanical stimuli and the deep anesthesia to the animals^[4,5]. Increasing studies on the dorsal column lemnisco-thalamic pathway in the mammalian brain, however, indicated that there were the convergences of sensory information in the somatosensory cortex^[6–8]. In addition, thalamic ventrobasal (VB) nucleus was also involved in converging sensory information in cat, raccoon and monkey^[9–11]. Thalamic VB nucleus is the

relay nucleus of somatosensory system, principally including the ventroposterolateral (VPL) nucleus and the ventroposteromedial (VPM) nucleus. It has been reported that there were also convergences of sensory information in the VPM of rats. For example, the VPM has quite large receptive fields (RFs) covering up to 20 but not only single whisker^[12–14]. However, whether a functional afferent convergence exists in rat VPL nucleus is still not clear. In order to answer this question, we used the single-unit extracellular recording method to study the properties of tactile responses of neurons at rat VPL nucleus.

2 Materials and methods

2.1 Animals and surgery Experiments were performed using 41 male Sprague–Dawley rats weighing 250–310 g (4–5 months). All procedures did as per principles of the National Institute of Health for the Care and Use of Laboratory Animals (NIH Publication No. 80-23, revised 1996). The animal was anaesthetized with 25% urethane (0.5 mL/100 g) through the entire experiment, and held on a stereotaxic apparatus. According to Paxinos and Watson's coordinate atlas of the rat, the parietal cortex was exposed by

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the craniotomy to penetrate the recording electrode in the thalamic VPL (AP -2.16–-3.84 mm, ML 2.4–3.5 mm, DV 5.4–7.0 mm). The animal was paralyzed by intraperitoneal injection of 0.5% Flaxedil (0.1–0.3 mL/h) and ventilated artificially during the experiment. Rectal temperature was monitored and maintained at $(38 \pm 0.5) ^\circ\text{C}$ with a thermostatic control pad.

2.2 Electrophysiological recording Single unit activity was recorded extracellularly in the VPL nucleus by means of glass micropipettes (impedance 3–8 M Ω) which was filled with 0.5 mol/L sodium acetate solution containing saturated fast green.

The tactile receptive field of a single VPL neuron was examined by a small hand-held brush. The quantitatively controllable tactile stimulus was delivered by an electronically gated solenoid with a probe of 1 mm in diameter as described previously^[15]. Spikes evoked by repetition (20 times) of the same tactile stimulation were averaged and the post-stimulus time histograms (PSTHs) were generated.

2.3 Histological identification After completion of the experiment, fast green was delivered to the recording sites from a glass micropipette by microelectrophoresis (10 μA for 30 min). The animal was perfused with the saline, fol-

lowed by 10% buffered formalin solution. After post-fixation (for 24 h), the brain was removed and was put into 10% buffered formalin solution with 5% potassium ferrocyanide for 2–7 d. Sixty micrometer-thick coronal sections were cut with a freezing microtome. The position of neuronal recordings was confirmed by microscopic examination. Location of the recording electrode was verified by histology. Figure 1 shows the sketch map of recording sites.

2.4 Statistical analysis The percentage of neurons of each type was analyzed for statistical significance by χ^2 test by using SAS 9.1.3 software. $P < 0.05$ was considered statistically significant.

3 Results

3.1 The receptive field of tactile neurons in rat VPL nucleus

As listed in Tab. 1, of the 156 VPL tactile neurons tested, 140 neurons (89.7%) had the single, continual and small receptive fields, while 16 neurons (10.3%) had two discrete receptive fields. Among the 140 neurons described above, the proportion of neurons with the single receptive fields in forelimb, hindlimb or trunk were 60% ($n = 84$), 30.7% ($n = 43$) and 9.3% ($n = 13$), respectively. Statistical analysis had shown that there was no significant difference in the percentage of neurons of each type with different properties (χ^2 test, $\chi^2 = 5.3$, $P > 0.05$).

3.2 Tactile responses of thalamic VPL neurons to static punctiform stimulation

Figure 2 was a series of recordings of a neuron with the large RF in trunk. When the tactile stimulation (indentation depth, 500 μm ; velocity, 49 $\mu\text{m}/\text{ms}$; duration, 1 000 ms) was delivered to the center of RF, it could evoke a strong ON-OFF response (Fig. 2A, B). However, the same tactile stimulus evoked a weak ON-OFF response (Fig. 2C-E) at other points within RF and induced only ON-response at the edge of RF (Fig. 2F-J). This result suggested that the same tactile stimulation evoked different discharge modalities at different points of the RF.

Fig. 1 Sketch map of recording location. Grey area shows recording location. VB, ventrobasal thalamus; VPL, ventroposterolateral thalamus; VPM, ventroposteromedial thalamus.

Tab. 1 RF distribution of VPL tactile neurons in rat thalamus

Types	Continual Receptive fields			Discrete Receptive fields		
	Forelimb	Hindlimb	Trunk	Forelimb Trunk	Trunk Hindlimb	Bilateral Trunk
Response to punctiform static tactile stimulation (number of neurons)	82	41	12	4	7	3
Response to locomotory tactile stimulation (number of neurons)	2	2	1	1	1	0
Total	84	43	13	5	8	3

Fig. 2 Tactile responses of a thalamic VPL neuron with the large RF in trunk. A-E: ON-OFF response to the tactile stimulation applied at or near the center of the receptive field; F-J: ON-response to the same tactile stimulation delivered to the edge of receptive field. K: Location of receptive field. The short bar under the abscissa represents tactile stimulation with 1 000 ms duration, 500 μ m indentation depth, 49 μ m/ms velocity. Post-stimulus-time-histograms: 20 stimulation repetition, 4 ms binwidth.

Figure 3 shows the recordings of a neuron with RFs in hindpaw. The tactile stimulation (indentation depth, 400 μ m; velocity, 60 μ m/ms; duration, 500 ms) evoked the ON-OFF response at pulvillus A, B of hindpaw (Fig. 3A, B) and ON-response at pulvillus C-F (Fig. 3C-F) and digit 1, 4 and 5 (Fig. 3G, J-K), while could not induce apparent responses at digit 2 (Fig. 3H) and digit 3 (Fig. 3I). These results also indicated that the RFs of VPL neuron were inhomogenous.

3.3 Tactile responses of thalamic VPL neurons to locomotory stimulation A few tactile neurons ($n=7$, 4.5%) of VPL nucleus did not respond to a static and punctiform tactile stimulation but did respond to brushing stimulation. These

neurons were classified as two groups. Group 1 neurons responded to brushing stimulation in all direction, being called as nondirection-sensitive neurons. Group 2 neurons responded to brushing stimulation in the certain direction, being called as direction-sensitive neurons.

Figure 4 was a record of a nondirection-sensitive neuron with RF in scapular region (Fig. 4H). A punctiform tactile stimulus did not evoke any related response (Fig. 4A), but this neuron produced the spikes to brushing stimulation in all directions in RF (Fig. 4B-G) and there was no significant difference in firing frequency to brushing stimulus in all directions within the receptive field.

Fig. 3 Tactile responses of a thalamic VPL neuron with RFs in hindpaw. A and B: ON-OFF responses to the stimulation applied to the pulvillus A, B of the hindpaw; C-F and G, J-K: ON-responses to the stimulation applied to the pulvillus C-F of the hindpaw and digit 1, 4 and 5; No response to the stimulation applied to digit 2 and 3. L: Location of RFs. The short bar under the abscissa represents tactile stimulation with 500 ms duration, 400 μ m indentation depth, 60 μ m/ms velocity. Post-stimulus-time-histograms: 20 stimulation repetition, 2 ms binwidth.

Fig. 4 Tactile responses of a nondirection-sensitive neuron to brushing stimulation. A: No response to the static and punctiform stimulation delivered to RF. B-G: Responses to brushing stimulation in different directions across the RF. H: Location of RF and directions of brushing stimulation. The arrow represents the direction of the brushing stimulation. Post-stimulus-time-histograms: 20 stimulation repetition, 2 ms binwidth.

Fig. 5 Tactile responses of a direction-sensitive neuron to brushing stimulation. A-D: Responses of the VPL neuron to brushing stimulation along the optimal direction in the receptive field. F-I: Responses of the same neuron to brushing stimulation in opposite direction. E: No response to punctiform stimulation applied to receptive field. J: Location of RF of the neuron and directions of brushing stimulation. The arrow represents the direction of brushing stimulation. Post-stimulus-time-histograms: 20-stimulus repetition, 2 ms binwidth.

Figure 5 shows a record of a direction-sensitive neuron. This neuron, similar to the described one above, did not respond to the static and punctiform tactile stimulus while responding to brushing stimulation in receptive field. The firing frequencies changed obviously when the direction of brushing stimulation was altered. As shown in Fig. 5, the responses to the brushing stimulation paralleling to the main axis of the body from fore to post (Fig. 5A) were stronger than those to the opposite direction (Fig. 5F).

4 Discussion

Thalamic ventrobasal nucleus, including mainly the VPL and the VPM, is the relay nucleus of somatosensory system. Many neurohistological and electrophysiological studies have shown that the representative areas of head, face, lip, tooth and lingua are in the VPM nucleus; while the contralateral limbs, trunk and tail are in the VPL nucleus. In addition, the volume of the nucleus in VPL and VPM

depends on the relative intensities of the somatosensory nerve allocated to the face and soma, respectively^[16-19]. In rodents, main tactile organs are the nose, whiskers and lips, thus the volume of VPM nucleus is larger than that of VPL nucleus, which has been studied well. In the present experiments, we focused our investigation on the VPL nucleus. As shown in Tab. 1, the proportion of neurons with receptive fields in the forepaw was the highest, next was in the hindpaw and the least was in the trunk.

It was proposed that there were various patterns of convergences of sensory information in the thalamic VB nucleus including the VPL and VPM nucleus in cat, raccoon and monkey^[9-11]. For instance, some neurons in thalamic VPL and VPM nucleus had large bilateral receptive fields^[19], which located in the hairy and glabrous skin area^[20]. These neurons were sensitive to locomotive stimulation, but not sensitive to the punctiform stimuli delivered to the receptive field^[21,22]. Werner and Whilse^[23] reported that there

were some “characteristic detectors” in the thalamic VPL and VPM nucleus, which were the same as the ones in somatosensory cortex, reflecting a convergent input.

In rodents, it has been reported that the VPM has quite large receptive fields covering up to 20 whiskers, which argues against the previous reports that the single receptive field in rat VPM covered only single whisker^[12-14]. These results suggest that there is convergence of tactile information in the VPM nucleus of rodent. However, it has not been known whether the convergence of tactile information also occurs in the VPL nucleus of rats. In the present study, we observed that properties of the vast majority of neurons in rat VPL nucleus mostly resembled those of peripheral tactile mechanoreceptors, such as responding to static punctiform stimulation and having the single and small RF. Notably, the minority of neurons in rat VPL nucleus had the large or two discrete RFs. These neurons produced the different responses to the same tactile stimulus delivered to different points in the RF, such as the center and edge of receptive field. The study suggested that there would be the ununiformity of receptive fields in rat VPL nucleus. In addition, some neurons in rat VPL nucleus were only sensitive to locomotive stimuli, but not sensitive to the static punctiform stimuli. This result is in agreement with the previous reports in monkey and cat, demonstrating that some neurons in rat VPL nucleus do not simply mimic peripheral receptor afferent, but converge afferents from different peripheral receptors. Therefore, it should be concluded that convergence of tactile information also occurs in the VPL nucleus of rats.

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大鼠丘脑腹后外侧核神经元触觉反应的特性

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摘要: **目的** 为确定大鼠丘脑腹后外侧核是否也发生触觉信息的会聚, 本文研究了大鼠丘脑腹后外侧核神经元触觉反应的特性。 **方法** 采用在体细胞外单位放电记录技术, 记录麻醉状态下大鼠丘脑腹后外侧核触觉神经元的放电活动。 **结果** 在记录的 156 个神经元中, 140 个神经元(89.7%)具有单一、连续的小感受野, 16 个神经元(10.3%)具有两个不连续的感受野。部分神经元对作用于感受野不同部位的相同触觉刺激产生不同的放电形式。此外, 还观察到 4.5% 触觉神经元($n = 7$), 它们仅对感受野内的运动性触觉刺激敏感, 而对点状触觉刺激不敏感。 **结论** 以上结果表明, 在大鼠丘脑腹后外侧核, 大多数神经元具有皮肤感受器的时空和模式特性, 而少数神经元表现出不同外周感受器相互作用的反应。由此可见, 大鼠丘脑腹后外侧核中存在触觉信息的会聚。 **关键词:** 丘脑; 腹后外侧核; 触觉反应; 感受野; 会聚