Tactile-Evoked Response of Sensory Fibers in Buccal and Submandibular Regions of the Rat

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Abstract Evoked neural responses to tactile stimulation were recorded electrophysiologically from the mechanoreceptive afferent fibers innervating the buccal and submandibular regions of Wistar rats anesthetized with sodium thiopental. Miniature probes 200 μm in diameter were used, and data analysis was performed on the mechanosensitivity of responses to tactile stimulation in the areas innervated by the mental, mylohyoid, auriculotemporal, and cervical nerves. Mechanosensitivity of each area showed a characteristic distribution of slowly adapting (SA), rapidly adapting (RA), C-fiber (CF), and hair follicle (HF) units in individual receptive fields. The density of the SA units was high in the areas innervated by the mylohyoid and auriculotemporal nerves. The CF units were concentrated in the small dome in the area of the mylohyoid nerve and the auriculotemporal nerve, as shown by a significant response to the dynamic features of stimulation. Estimation of the current needed for tactile acuity suggests an important role of the SA fibers in the areas innervated by the auriculotemporal, mylohyoid, and cervical nerves.

Key words tactile, afferent fiber, mechanoreceptor, buccal region, submandibular region, slowly adapting fiber

The skin is a multisensory structure. In the present study, the contribution of mechanoreceptors to the peripheral aspects of sensory perception was evaluated by examining and comparing their ability to resolve fine detail among the areas innervated by the mental, mylohyoid, auriculotemporal, and cervical nerves. Characteristic differences in the sensitivity of these locations to peripheral mechanical stimulation were investigated by analyzing discharges from afferent nerve fibers innervating the face and neck.

METHODS

Forty Wistar rats aged 8–10 weeks were anesthetized with sodium thiopental without tracheal cannulation. Body temperature was maintained at 37–38°C with a heating pad. An operating microscope and fine microsurgical instruments were used. The mental, mylohyoid, cervical, and auriculotemporal nerves were exposed at the mental foramen, submandibular region, clavicular bone, and buccal area, respectively. For spike recording, each nerve was severed, and the single fibers of its peripheral cut end at the levels of the abovementioned positions were placed on fine blunt tungsten hook electrodes (resistance > 2 MΩ) as described previously (Furusawa et al., 1992). The recording electrodes were connected to a high-input impedance preamplifier and a main amplifier (AVH-10, Nihon Kohden), and the impulses were displayed on an oscilloscope (VC-10, Nihon Kohden). The afferent discharge and stimulus force were simultaneously recorded on a magnetic tape recorder. The analog signals were digitized and processed with an NEC PC-9800 computer system.

The mechanical stimulus consisted of tactile stimulation of the skin of the face and neck, and of the guard hairs in the mental region, with a blunt glass probe 200 μm in diameter. The force was applied perpendicular to the skin, with a contact force of 10 mN and an initial velocity of 25 mN/sec, using a moving coil transducer. With these selections, responses of slowly adapting (SA), rapidly adapting (RA), C-fiber (CF), and hair follicle (HF) units to stimulation were obtained. Stimulus duration was less than 2 sec and

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interstimulus intervals were 15 sec, in order to minimize the effects of adaptation of the fibers. The effects of tactile stimulation on afferent responses were assessed from the value of interspike interval distributions of discharge following tactile stimulation to the skin, or fillip stimulation to the guard hairs. The position of receptive spots was mapped in each field innervated by four nerves, and the number of spots showing each discharge type was determined in each individual trial.

Our criteria for SA (types I and II), RA, CF, and HF units were based upon the classification of Ferrington (1985).

RESULTS

The distribution of the sites responding to tactile stimulation was as follows. The receptive field of the mental nerve was delineated cranially by the lower lip and midline, and caudally by the mandibular border. The receptive field of the mylohyoid nerve was delineated cranially by the caudal border of the mental nerve and its midline, and the region innervated by the communicating branch of the auriculotemporal nerve; it was delineated caudally by the line corresponding to the first molar. The receptive field of the transverse cervical nerve was delineated cranially by the caudal border of the mylohyoid nerve and its midline and the infra-auricular region, and caudally by the clavicular bone. The receptive field of the communicating branch of the auriculotemporal nerve was delineated anteriorly by the corner of the lip, superiorly by the infraorbital region, posteriorly by the parotis masseter region, and inferiorly by the mandibular border. Mapping of the receptive fields is shown in Figure 1.

Although the bursts were related to sensitivity to the tactile stimulus, receptive fields did not always respond equally to tactile stimulation, and sensitive parts were relatively more common within the fields. However, all areas were included in the investigation of stimulus location in the present study. Impulse responses to stimulation of hairy skin were recorded in 156 single mechanoreceptive units. SA (types I and II), RA, CF, and HF fibers were found in the buccal and submandibular regions (Fig. 2). Interspike interval distributions of each type are illustrated in Figure 2. SA units of both types were clearly differentiated by their interspike interval distributions. Discharge of CF units converged with the SA units' response to stimulation. There was a lag of onset of discharge in the CF units of 85 ± 30 msec ($n = 11$), compared with the onset of discharge in the SA units. The numbers and percentages of each type of unit of neural discharge found in each area are shown in Table 1. These results may explain the difference in frequency of the responses to tactile stimuli between each area. The SA units were largely observed in the areas innervated by the auriculotemporal, mylohyoid, and cervical nerves, and less in areas innervated by the mental nerve. The CF units were found in the domes, which were 300–400 μm in diameter, in the area innervated by the auriculotemporal and mylohyoid nerves. The RA units were found in the area innervated by the auriculotemporal, mylohyoid, and cervical nerves. The HF units were only observed in the area of the mental nerve. Thus, the mental region was found to be relatively unresponsive to tactile stimulation of the skin, whereas an increased

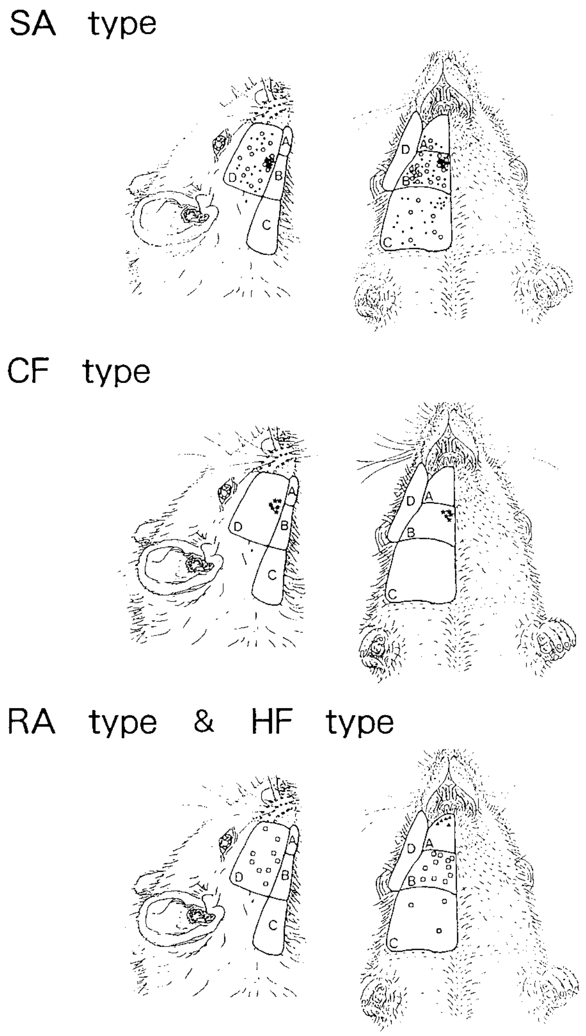

FIGURE 1. Receptive fields and spatial distribution of units mapped on schemaic drawings of the face and neck. Shown are receptive fields innervated by the (A) mental nerve, (B) mylohyoid nerve, (C) cervical nerve, and (D) auriculotemporal nerve. Open circles, SA type I units; filled circles, SA type II units; stars, CF units; open squares, RA units; filled triangles, HF units.

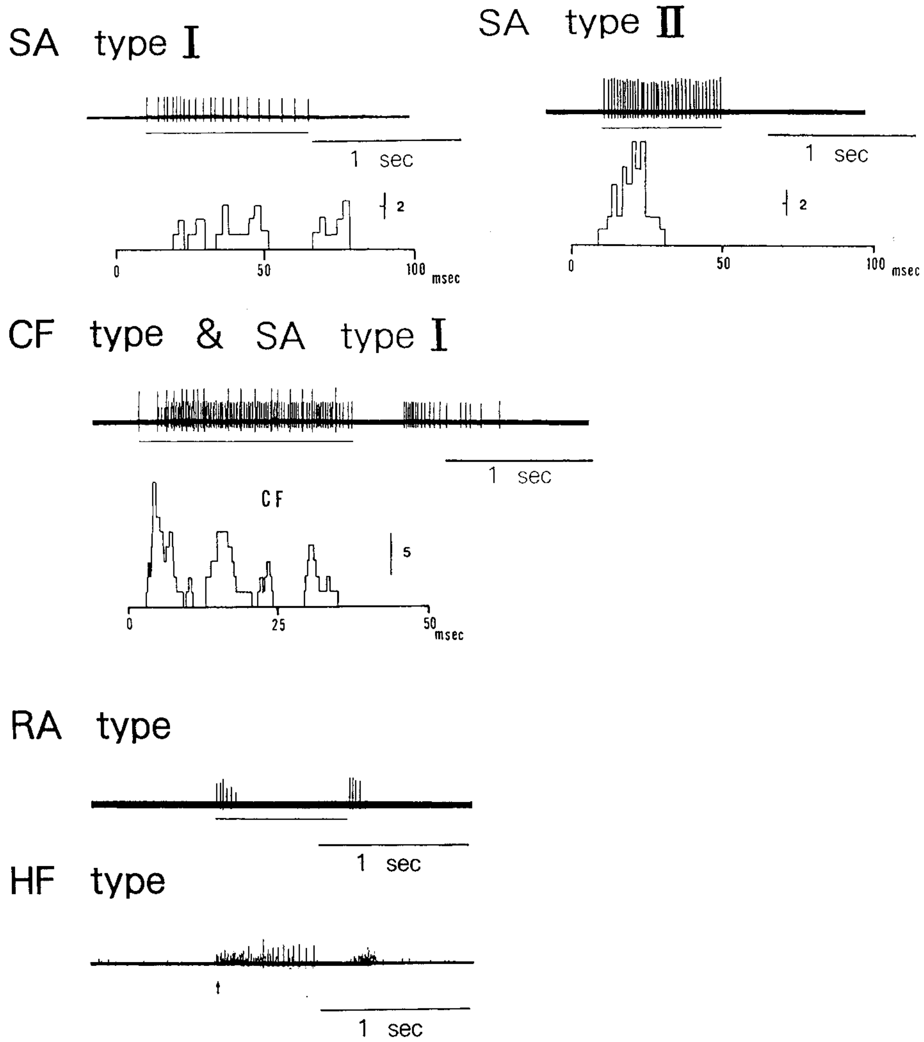

FIGURE 2. Types of typical neural discharges observed in the buccal and submandibular regions. SA and CF units' interspike interval distributions were added during stimulation. The CF units converging with SA type I units are shown by high voltage and are responding to stimulation, and a time lag of the onset of the CF units, which exhibited afterdischarge following mechanical stimulation, is clearly seen. Periods of stimulation to the hairy skin are indicated by solid lines below discharges. Fillip stimulation is indicated by an arrow. Calibration: Vertical bar represents 2 or 5 discharges or impulses.

TABLE 1. Numbers and Percentages (in Parentheses) of Units Observed in Individual Regions

	SA		CF	RA
	Type I	Type II		
Mental nerve ($n = 5$)	2 (40.0)	3 (60.0)	—	—
Mylohyoid nerve ($n = 63$)	18 (28.6)	29 (46.0)	5 (7.9)	11 (17.5)
Auriculotemporal nerve ($n = 57$)	14 (24.6)	28 (49.1)	6 (10.5)	9 (15.8)
Cervical nerves ($n = 31$)	6 (19.4)	22 (71.0)	—	3 (9.7)

rate of discharge was evoked by stimuli to the guard hairs controlled by the mental nerve. Unit density of SA type I fibers was high in the areas innervated by the mylohyoid, auriculotemporal, and cervical nerves, whereas RA units were less frequent than SA units in these areas. There were 6 SA type I units (19.4%) and 22 SA type II units (71.0%) in the area innervated by the cervical nerve. The relative percentages of CF units were 7.9% and 10.5% in the areas innervated by the mylohyoid nerve and auriculotemporal nerve, respectively.

These findings indicate that the afferent discharge in each area exhibited distinctive features, according to the stimulus force. Moreover, although the discharges of SA units elicited by the tactile stimulation were not significantly different for the mylohyoid, auriculotemporal, or cervical nerves, the SA units were most frequently found.

DISCUSSION

The rate of change in momentum is related to the net force, the stimulus duration, and the interstimulus intervals. If either the stimulus duration is too long or the interstimulus intervals are too short, there is a progressive decline in effective force from one trial to the next, since recovery is not complete by the time of onset of the next trial (Pubols, 1982). Constant stimulus duration and interstimulus interval, as well as contact force and initial velocity, were used in the present study. We assumed that the neural response was reflected by the spike after minimal repetitions.

The present study revealed the characteristics of afferent discharges in the buccal and submandibular regions, although the receptive field properties introduce a bias, becoming relatively homogeneous over the total skin area. However, it is possible to observe the locations of the receptive fields of individual units and the relative unit densities within various skin regions, and these fields have been demonstrated in the palm and the finger (Johansson and Vallbo, 1979). The differences observed between individual areas appear to be essential for the accurate recognition of actual response profiles evoked by stimulation, with simultaneous inputs observed from different receptors representing a basic neural mechanism modulated in the central system by the interaction of multiply activated fibers with any single or complex stimuli.

The data presented in this report indicate that receptive field properties differ in individual regions. Units with five different response characteristics were evoked by the stimuli. The genesis of different response patterns to a particular complex of stimuli is the result of multiple sensory systems' being present in a single area. The activity of CF units could be distinguished clearly from background activity. This might be attributable to a low-threshold mechanoreceptor in the CF units (Douglas and Ritchie, 1957; Iggo, 1960; Bessou et al., 1971) and the slow conduction velocities of these units (Bessou et al., 1971). There are receptive elements of unmyelinated CF units that have a unique response to the dynamic features of a stimulus, and Bessou et al. (1971) showed them (1) to be numerous in nerves innervating the hairy skin of the cat; (2) to have small receptive fields; (3) to exhibit afterdischarges following mechanical stimulation; (4) to fatigue when repeatedly stimulated; (5) to be excited by cooling; and (6) to have the same peak frequency regardless of the indentation rate, except for very low velocities. The conduction velocities of CF mechanoreceptor units were 0.5–1.1 m/sec in the dorsal root and 0.6–1.2 m/sec in the posterior femoral cutaneous nerve (Bessou et al., 1971), whereas those of SA units were 54–72 m/sec (Tasaki and Ogawa, 1989). The present finding of a lag of onset of discharge in the CF units of 85 ± 30 msec ($n = 11$), compared with the onset in SA units (Fig. 2), is consistent with their conduction velocities.

Although the burst response to tactile stimulation was pronounced in the guard hairs in the mental region, there was marked insensitivity in response to mechanical displacement of the skin. This indicates that the role of the guard hairs in gathering tactile information is especially important compared with that of the skin in the mental region in rats. Thresholds may be higher for the mental nerve in the skin, or there may be fewer mechanoreceptors in the mental skin than in the guard hair follicles.

Responses were strongest at the domes in the small receptive fields. The "touch spots" are raised, roughly hemispherical domes in the skin of the thigh, leg, and foot in the cat and rabbit (Iggo, 1963). The touch corpuscle units are normally silent in the absence of an intentionally applied stimulus (Iggo and Muir, 1969). Such spots were also located in the skin of the buccal and submandibular regions in the rat and included CF units, which contain low-threshold mechanoreceptive units. These spots, which are covered with hair and consist of many SA units, have high sensitivities and may be involved in sensorimotor activities regulating muscle contraction of the face and neck during ingestion and mastication or suckling in the neonatal period. However, their role is unclear and requires further investigation. Our results are in contrast to the data from the study of Johansson and Vallbo (1979), in which roughly one-half of the high-sensitivity mechanoreceptive units in the glabrous skin were found to be RA, both in monkeys and in humans. Many of the SA type II units are spontaneously active (Johansson and Vallbo, 1979), and may be involved in motor control processes showing proprioceptive features (McCloskey, 1974; Hulliger et al., 1979; Westling and Johansson, 1987). Those in the buccal and submandibular regions, especially in the area innervated by the cervical nerve, may be related to the support of external and internal activities, such as swallowing, upper airway patency, and other movements.

Thus, the responses to constant stimuli in each area did not always exhibit uniform sensitivity. This feature may be essential for the sensitivity relayed by cutaneous receptors to contribute to the identification of an object via fine tactile stimulation. Although the multiplicity of tactile responses in each area must be integrated, so that summation and/or surround inhibition of sensory afferent inputs from any sensory terminals of all areas around the mouth can be centrally unified and match the functions of the mouth, analysis of such neural discharge will help to provide a clear understanding of the basic concepts of this critical determinant of orofacial behavior.

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