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Research Note

Mechanoreceptor activity from the human face and oral mucosa

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Summary. The feasibility of adopting the microneurography technique (Vallbo and Hagbarth 1968) as a tool to investigate the mechanoreceptive innervation of peri- and intra-oral tissues was explored. Multi-unit activity and impulses in single nerve fibers were recorded from the infraorbital nerve in healthy volunteers. The innervation territories of individual nerve fascicles were mapped. These varied considerably but most fascicle fields comprised the corner of the mouth. Twenty-four single mechanoreceptive units were recorded. Eighteen innervated the skin of the face, and six innervated the mucous membranes of the lips or cheeks. A majority of the mechanoreceptive afferent units were slowly adapting with small and well defined receptive fields. It is suggested that the various slowly adapting responses may originate from two different types of afferent units. No afferents showed response properties similar to typical Pacinian-corpuscle afferents.

Key words: Mechanoreceptors – Man – Face – Infraorbital nerve – Microneurography – Trigeminal nerve – Tactile sensibility – Cutaneous sensibility – Oral mucosa

Introduction

Using tungsten microelectrodes, Vallbo and Hagbarth (1968) demonstrated an elegant method of recording sensory impulses transmitted in human peripheral nerves in situ. Using this technique, the first analysis of functional properties of mechanoreceptive units in the peripheral trigeminal afferent system in man was made in 1976 (Johansson and Olsson 1976). In that study of mechanoreceptive afferents in the inferior alveolar nerve, a few periodontal afferents were analyzed. Afferents with receptive fields located in the cutaneous and transitional zones of the lip were also described. Since then, Nordin et al. (1983) have recorded afferent activity from rapidly and slowly adapting mechanoreceptors in the trigeminal system in man, though no full paper has yet been published. The aim of the present study was to further explore the feasibility of adopting the microneurography technique as a tool to investigate the mechanoreceptive innervation of the peri- and intra-oral tissues. The infraorbital nerve was chosen primarily because of its accessibility. This nerve innervates the lower eyelid, skin and mucous membranes of the cheek and upper lip.

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Methods

Experiments were performed on both left and right infraorbital nerves of two healthy volunteers (male subjects, 25 and 45 years old). The subject sat comfortably in a dentist's chair. A tungsten microelectrode (Vallbo and Hagbarth 1968) was used to impale the nerve close to its exit from the infraorbital foramen (electrode impedance 160–310 kΩ at 1000 Hz, in situ). To protect the insulation and the tip of the electrode during insertion, a small hole was first made through the skin using a hypodermal cannula. Care was exercised not to deform the tip of the electrode by contacting the maxillary bone. Multi-unit activity and impulses in single nerve fibers were recorded.

A set of calibrated von Frey hairs (0.25, 0.5, 1, 2, 4, 8, 16, 32 and 60 mN) were used manually to apply mechanical stimuli to the skin of the face and oral mucosa (cf. Johansson et al. 1980). Local taps and more firm indentations of the skin and the mucosa were applied using hand held blunt glass probes. When desired, the prodding forces could be continuously measured using a separate set of von Frey hairs (15, 40, 75 mN) that were mounted on handles equipped with force transducers (DC-120 Hz). The experimental data were recorded on analog magnetic tape (DC-2.5 kHz) and were later displayed on an electrostatic chart recorder (DC-10 kHz). A record of the instantaneous discharge frequencies of single units was obtained by feeding the nerve signal into a spike discriminator (Edin et al. 1987) and thence to an interspike-interval-to-voltage converter.

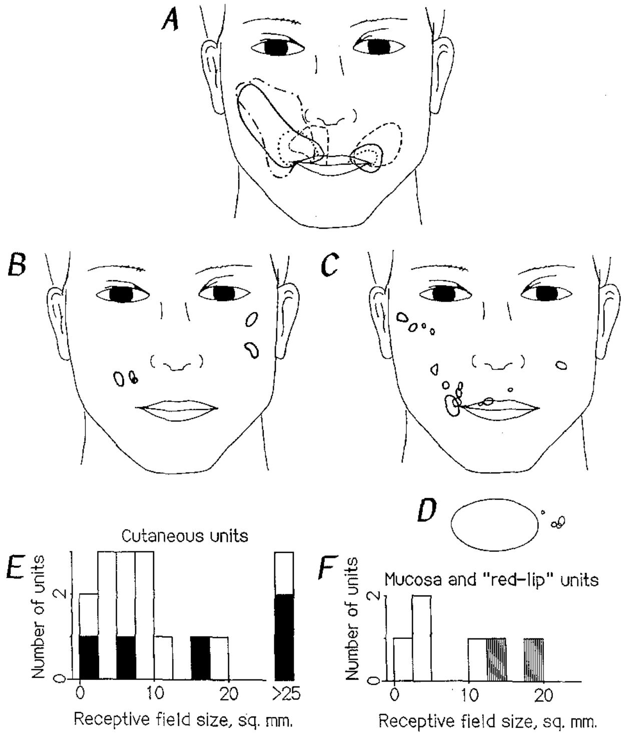

Fig. 1. Receptive fields of nerve fascicles (**A**) and single tactile afferents (**B–F**) identified in records from the infraorbital nerves. **A** Receptive fields for mechanically evoked multi-unit responses from seven nerve fascicles. Some of these fields extended intraorally as described in the text. Data from two subjects superimposed. **B–F** Receptive fields of 23 mechanoreceptive afferent units. **B–D** Schematic drawings showing the location of the fields of rapidly adapting cutaneous afferents (**B**), slowly adapting afferents in the skin and transitional zone of the upper lip (**C**), and slowly adapting mucosal afferents (**D**). The ellipsoid in **D** indicates the contour of lips with the mouth open and parts of the lips and buccae are schematically viewed from within the mouth. **E** and **F** Distribution of sizes of receptive fields. **E** Black and white columns refer to rapidly adapting units and slowly adapting units with cutaneous fields, respectively. **F** White and hatched columns refer to slowly adapting units with fields in the mucosa and transitional zone of the upper lip, respectively

Results

Fascicle innervation territories. Innervation territories of seven nerve fascicles were mapped during multi-unit recording (cf. Hagbarth et al. 1970). These territories were defined as the cutaneous and/or intraoral areas which were associated with detectable mass responses during prodding with a 60 mN von Frey hair. For purposes of this assessment, nerve activity was monitored using earphones and an oscilloscope. Figure 1 shows the cutaneous innervation territories. Although their sizes varied considerably, the extent of the fascicular fields were not found to be influenced appreciably when von Frey hairs having either twice or half of the nominal 60 mN force were tested. The largest fascicle fields extended from the corner of the mouth to the inferior and lateral borders of the orbit covering a considerable part of the cheek and the upper lip. The smallest field was a ca. 1.5 sq. cm patch encircling the corner of the mouth. Only one field was found that did not include the corner of the mouth. Most fascicles with fields mainly confined to the upper lip innervated the corresponding mucosal area of the lip. The fascicle with the largest cutaneous field also innervated a mocosal area. However, for this fascicle the mucosal field was much smaller than the cutaneous area. It included the lateral portion of the upper lip and a ca. 2 sq. cm of the adjacent buccal mucosa. No fields were found which crossed the midline of the face. However, as may be seen in Fig. 1, some fascicle fields extended into the classical mandibular dermatome (cf. Warwick and Williams 1973) suggesting a strong overlap between this dermatome and the maxillary dermatome.

Recordings of multi-unit activity showed little activity in the absence of intentionally applied stimulation. In response to skin/mucosa deformation, the dynamic response strongly predominated over the static response, and distinct "on-" and "off"-discharges were observed at the beginning and at the end of a maintained indentation. Vigorous responses were induced by mechanical stimuli moving along the skin surface.

Single unit sample. Impulse responses were recorded in twenty-four single mechanoreceptive units. For eighteen of these units, cutaneous receptive fields could be identified. Twelve of the cutaneous units adapted slowly in the sense that they sustained a tonic discharge for more than ca. 2 s during a firm maintained indentation of the field. The remaining six units adapted rapidly, i.e. they responded exclusively to changes in skin deformation. One cutaneous afferent responded to manipulation of a single hair of the moustache of one of the subjects. This unit only discharged during movements of the hair and not to a maintained hair stimulus. Four units had receptive fields in the intraoral mucosa and two had receptive fields in the transitional zone of the upper lip. These six units were all slowly adapting. The extent of the receptive fields of the cutaneous and the mucosal units was defined with von Frey hairs at 4 times the threshold of the unit (Johansson and Vallbo 1980).

Rapidly adapting units. Figure 1B shows schematically the location and sizes of the receptive fields of the rapidly adapting cutaneous units (the "hair" afferent is not shown) whereas the filled columns in the histogram of Fig. 1E show the sizes of these fields

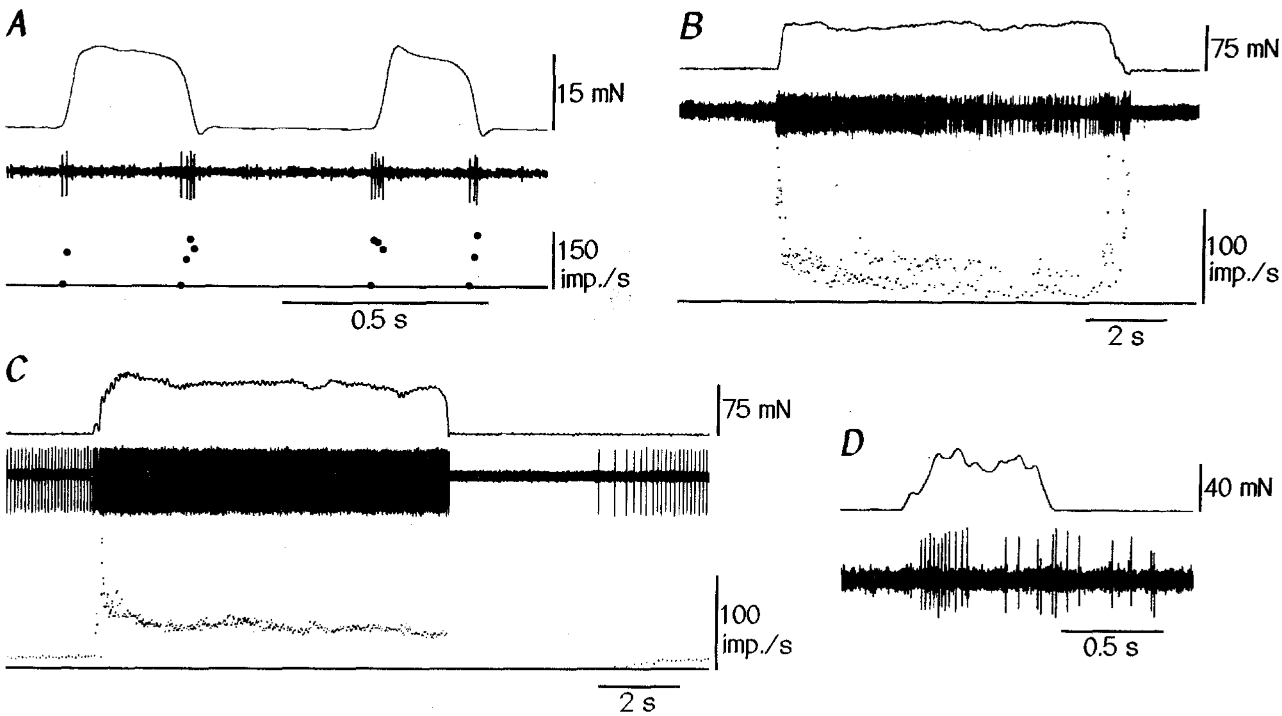

Fig. 2A–D. Four types of discharge patterns observed in mechanoreceptive afferents in records from the infraorbital nerves. Local pressure was delivered to the receptive field of the units with von Frey hairs equipped with force transducers to measure the actual force. **A–D** Responses in four separate units. Top traces show the applied force. Below is shown the neurogram and the instantaneous discharge frequency (except in **D**). **A** Rapidly adapting unit with a receptive field (7 sq. mm) located in the skin of the upper lip. Threshold 0.25 mN. Note the "on"- and "off"-responses at the onset and retraction of the stimulus, respectively. **B** Slowly adapting unit with a receptive field (12 sq. mm) located in the oral mucosa. Threshold 1 mN. Note the pronounced "off"-response at the retraction of the stimulus and the irregular discharge during the static phase of the stimulus. **C** slowly adapting unit with a punctate receptive field (3 sq. mm) in the skin at the corner of the mouth. Threshold 2 mN. Note the ongoing response in the absence of externally applied stimulus, the regular discharge during the static phase of the stimulus and the pause after the stimulus. **D** Slowly adapting unit with the receptive field (9 sq. mm) located in skin of the cheek ca. 3 cm below the lateral edge of the orbit. Threshold 1 mN. Note the pronounced discharge after the cessation of the stimulus

(median, 17 sq. mm; range: 2–118 sq. mm). Most fields were made up of an approximately circular or oval well defined area of high and relatively uniform sensitivity. The fields of some units were found to possess more than one zone of maximal sensitivity during the von Frey hair stimulation. None of the rapidly adapting skin afferents were activated by taps applied at sites remote to the receptive fields, indicating that the sampled units did *not* contain Pacinian corpuscle afferents (cf. Hunt and McIntyre 1960; Johansson and Vallbo 1979). All rapidly adapting units showed burst responses at the beginning and end of a sustained skin indentation (Fig. 2A). Sometimes the "off"-response was stronger than the "on"-response. With graded von Frey stimuli, stiffer hairs produced stronger responses. The maximum instantaneous discharge frequencies obtained in response to sudden skin displacement were ca. 200–400 imp./s (varied among the units). The threshold as determined with von Frey hairs ranged between 0.25 and 4 mN (median, 0.5 mN).

Slowly adapting units. Figure 1C and D show schematically the receptive fields of the slowly adapting afferents. The white columns in the histograms of Fig. 1E show the sizes of the cutaneous fields whereas Fig. 1F shows the sizes of the mucosal fields (white columns) and the fields of the units in the transitional zone of the lip (hatched columns). There were no obvious differences in field sizes between the cutaneous units (median, 7 sq. mm; range, 2–88 sq. mm) and the mucosal/transitional units (median, 8 sq. mm; range, 2–19 sq. mm). As with the rapidly adapting units, most fields were made up of an approximately circular or oval well demarcated area of high and relatively uniform sensitivity.

All slowly adapting units showed a dynamic response to the onset of the mechanical stimulus. The maximum discharge frequencies obtained in response to rapid skin displacements were ca. 150–500 imp./s. Moreover, nine slowly adapting units showed dynamic "off"-discharges similar to those exhibited by the rapidly adapting units (Fig. 2B). The maximum response rates during maintained punctate pressure were ca. 30–110 imp./s and increasingly stiffer von Frey stimuli evoked stronger responses. More than half of the slowly adapting units (10/18) exhibited an irregular discharge pattern during maintained tissue deformation (Fig. 2B) whereas the remainder showed a remarkably regular firing (Fig. 2C). In contrast to the rapidly adapting units some of the slowly adapting units (6/18) were spontaneously active, i.e. they showed an ongoing responses in the absence of externally applied mechanical tissue deformation. The von Frey threshold for the cutaneous units ranged between 0.25 and 4 mN (median, 1 mN) and between 0.5 and 2 mN (median, 1.5 mN) for the mucosal and transitional units. Thus, there were no obvious differences in threshold sensitivities of the rapidly and slowly adapting units. With spontaneously active units, the threshold was defined as the minimum force which caused a clear modulation of the ongoing response.

Further analysis suggested that the slowly adapting responses may originate from at least two different types of afferent units. One unit type is characterized by regular firing and often shows spontaneous activity as illustrated in Fig. 2C. Only one of the units that showed regular firing, also showed an "off"-response (1/8) whereas five of the six spontaneously active units showed regular firing. Another type of unit, illustrated in Fig. 2B, is characterized by an irregular static discharge, a proneness for "off"-responses: eight of the units with irregular firing (8/10) showed "off"-responses and only one discharged spontaneously (1/10). Moreover, units of this kind often also showed higher peak discharge rates (up to 500 imp./s) than the units with regular firing (peak rates < 240 imp./s). Units showing each of these discharge patterns were observed in both subgroups of cutaneous and mucosal/transitional units.

One highly sensitive cutaneous slowly adapting unit (threshold 1 mN) showing irregular static discharges and "off"-responses differed from the others in two respects. First, it showed a considerable delay (minimum ca. 50 ms) between the onset of the force stimulus and the appearance of the action potentials. This was true also with rapid prodding using the stiffest von Frey hair. This delay may have been due to a low conduction velocity of the afferent fiber and/or a slow transducer process. In the latter case, it might be expected that the delay would be reduced when the skin was stimulated by rapid prodding using a stiffer von Frey hair. This, however, was not the case. If the initial response delay was solely due to slow afferent conduction the conduction velocity would have been ca. 1 m/s (conduction distance ca. 5 cm). Second, after the withdrawal of the stimulus there was a gradually declining after-discharge which lasted for up to ca. 1 s. This after-discharge did not correspond to any visible slow mechanical skin recovery after the stimulus.

Discussion

The present findings suggest that the majority of the mechanoreceptive afferent units in the skin of the human face are slowly adapting with small and well defined receptive fields. Likewise, we found only slowly adapting units in the oral mucosa and the transitional zone of the lip. This is in agreement with our earlier findings of the oral innervation in man (Johansson and Olsson 1976), but in some contrast to results from animal studies (Sakada 1983; Appenteng et al. 1982a, b; see also Landgren and Olsson 1982). The properties of the tactile units in the human infraorbital nerve showed some similarities to those of four of the five types of tactile afferents innervating the skin of the hand, i.e. hair follicle units and three types of units described in the glabrous skin (FA I, SA I and SA II units) (for refs. see Vallbo et al. 1979; Vallbo and Johansson 1984). With regard to the slowly adapting units, units with a high dynamic sensitivity and an irregular impulse train during maintained tissue deformation resemble the slowly adapting type I units (SA I) in the hairy and glabrous skin in man. However, strong "off"-responses have not been described for the latter units. The other group of slowly adapting units, characterized by a regular discharge rate and spontaneous activity are similar to the slowly adapting type II (SA II) units. An important feature of SA II units is an exquisite sensitivity to lateral skin stretch applied far away from the zone of maximal sensitivity (Knibestöl and Vallbo 1970; Chambers et al. 1972). Lateral stretching of the skin was avoided in the present study, however, because it often dislocated the electrode causing the unit under study to be lost. One slowly adapting cutaneous afferent in the present sample may have been a non-myelinated C-fiber as judged from the exceptionally long delay between the mechanical stimulation and the recorded nerve response. Indeed, the response characteristics of this unit showed striking similarities with those of highly sensitive mechanoreceptive units with non-myelinated afferents described in the hairy skin of cat and monkey (Iggo 1960; Iggo and Kornhuber 1968; Kumazawa and Perl 1977), i.e. "on"- and "off"-responses and after-discharges. Low-threshold mechanoreceptors with these characteristics have not previously been described in man (e.g. Vallbo et al. 1979). Regarding the few rapidly adapting units in the present sample, their properties, as crudely defined by hand held instruments, resembled those of the fast adapting type I (FA I) units in the glabrous skin. No afferents showing response properties similar to typical Pacinian-corpuscle afferents were observed (cf. fast adapting type II (FA II) units in the glabrous skin). This is in agreement with recent neurophysiological findings in the rabbit (Appenteng et al. 1982a, b) and psychophysical findings in man (Barlow 1987). Barlow concludes that "pacinian-type frequency sensitivity, characteristic of the finger, was absent in the face".

It is well established that the oral and perioral regions have an outstanding tactile spatial acuity as determined by psychophysical methods (e.g. Weinstein 1968). A critical factor for the resolving power of the peripheral tactile system is the density of afferent units and the properties of the receptive fields. The sizes of the receptive fields observed in the present experiments were approximately the same or somewhat smaller than those of tactile afferents innervating the glabrous skin of the finger tips (Johansson and Vallbo 1980). The high overlap of fascicle fields in the angle of the mouth suggests that the perioral area is the most densely innervated cutaneous area. Likewise, the spatial distribution of the receptive fields of the afferent units in the present sample, particularly the slowly adapting units, supports this idea. Similar distributions of receptive fields of tactile afferents have been shown in studies of the rabbit's face (Appenteng et al. 1982a).

The present study clearly demonstrates that somatic sensory mechanisms of the human face and mouth may be a profitable area for further, more extensive investigation using microneurography. As will be demonstrated in the accompanying paper, with this technique it is also possible to analyze afferent signals which arise during speech gestures and chewing (Johansson et al. 1988).

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