Sensations Evoked by Microstimulation of Single Mechanoreceptive Afferents Innervating the Human Face and Mouth

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Trulsson M, Essick GK. Sensations evoked by microstimulation of single mechanoreceptive afferents innervating the human face and mouth. J Neurophysiol 103: 1741–1747, 2010. First published February 3, 2010; doi:10.1152/jn.01146.2009. Intraneural microneurography and microstimulation were performed on single afferent axons in the inferior alveolar and lingual nerves innervating the face, teeth, labial, or oral mucosa. Using natural mechanical stimuli, 35 single mechanoreceptive afferents were characterized with respect to unit type [fast adapting type I (FA I), FA hair, slowly adapting type I and II (SA I and SA II), periodontal, and deep tongue units] as well as size and shape of the receptive field. All afferents were subsequently microstimulated with pulse trains at 30 Hz lasting 1.0 s. Afferents recordings whose were stable thereafter were also tested with single pulses and pulse trains at 5 and 60 Hz. The results revealed that electrical stimulation of single FA I, FA hair, and SA I afferents from the orofacial region can evoke a percept that is spatially matched to the afferent’s receptive field and consistent with the afferent’s response properties as observed on natural mechanical stimulation. Stimulation of FA afferents typically evoked sensations that were vibratory in nature; whereas those of SA I afferents were felt as constant pressure. These afferents terminate superficially in the orofacial tissues and seem to have a particularly powerful access to perceptual levels. In contrast, microstimulation of single periodontal, SA II, and deep tongue afferents failed to evoke a sensation that matched the receptive field of the afferent. These afferents terminate more deeply in the tissues, are often active in the absence of external stimulation, and probably access perceptual levels only when multiple afferents are stimulated. It is suggested that the spontaneously active afferents that monitor tension in collagen fibers (SA II and periodontal afferents) may have the role to register the mechanical state of the soft tissues, which has been hypothesized to help maintain the body’s representation in the central somatosensory system.

INTRODUCTION

The technique of percutaneous microneurography was introduced 40 years ago and demonstrated that the electrical activity of individual mechanoreceptive afferents in peripheral sensory nerves could be recorded from awake human subjects (Knibestol and Vallbo 1970; Vallbo and Hagbarth 1968). The pioneering recordings were obtained from the median and ulnar nerves of the hand and revealed that the response of afferents could be classified as fast adapting (FA) or slowly adapting (SA) to punctate stimuli pressed into the skin and that some afferents (type I) have small well-defined receptive fields (RFs), whereas others (type II) exhibit large RFs with obscure borders (Vallbo and Johansson 1984).

Fifteen years after the introduction of percutaneous microneurography, it was first demonstrated that individual mechano receptors of each of the four classes described in the glabrous skin (FA I, FA II, SA I, and SA II), in addition, could be electrically stimulated by the same electrodes used to characterize the afferents’ response to natural stimuli applied to their receptive fields (Ochoa and Torebjörk 1983; Vallbo et al. 1984). With the exception of SA II afferents, the microstimulation often produced sensations at a location and over an area of skin that closely paralleled the location and area of the afferents’ RFs. Moreover, microstimulation of FA I units with pulse frequencies within the 20–40 Hz range usually produced sharply localized sensations of flutter. In contrast, stimulation of SA I units at the same frequencies usually produced more diffuse sensations of noncyclic pressure or inward pulling of the skin. Changes in stimulus frequency altered the pitch of the flutter sensation (FA afferents) and the magnitude of the pressure/pulling (SA I afferents) (Ochoa and Torebjörk 1983; Torebjörk et al. 1987; Vallbo et al. 1984). More recent studies using a dense array of electroencephalographic (EEG) scalp electrodes (Kelly et al. 1997) and functional magnetic resonance imaging (fMRI) (Trulsson et al. 2001) have shown additionally that microstimulation of single FA I and SA I afferents in the hand evoke discrete patterns of cortical activation that are topographically appropriate.

The present study sought to determine if percepts could be evoked by microstimulation of single mechanoreceptive afferents in the orofacial region. To this end, individual mechanoreceptive afferents in the inferior alveolar and lingual nerves were microstimulated after the response properties of each had been studied with natural mechanical stimuli applied to the face, teeth, labial, or oral mucosa. Microstimulation of single FA I, FA hair, and SA I afferents was found often to evoke a percept that was spatially matched to the afferent’s receptive field and consistent with the afferent’s response properties as observed on natural mechanical stimulation. In contrast, microstimulation of single periodontal, SA II, and deep tongue afferents failed to evoke a sensation that matched the receptive field of the afferent.

METHODS

Subjects

Microneurography and microstimulation were performed on 10 healthy volunteers (4 males, age: 22–30 yr; 6 females, age: 20–26 yr), who participated in experimental sessions lasting 3–5 h each. All subjects were completely unaware of the hypotheses being tested. Prior to every session, the nerve recording and stimulation techniques were fully explained, and informed consent was obtained in accordance with the Declaration of Helsinki. The study was reviewed and approved by the local ethical committee at the Karolinska Institute.
The subject was comfortably seated in a dental chair. A trimmed thermoplastic block was placed between the upper and lower molars of one side to keep the mouth open in a stable position. A horizontal plate attached to the thermoplastic block restricted upward movement of the tongue and prevented contact between the tongue and electrode (Trulsson et al. 1992). Because the plate covered only the middle third of the tongue, the anterior third and tip remained free for manipulation. Saliva was evacuated as needed from the mouth with a syringe. Clinical asepsis was maintained. A chart was placed in the subject's reach on which he/she could indicate the occurrence of altered sensations (paresthesia, pain, etc.) during manipulation of the microelectrode as well as the quality and location of the percepts evoked during microstimulation.

**Microneurography procedure**

Nerve recordings from the inferior alveolar nerve or the lingual nerve were made using techniques similar to that described previously (Johansson and Olsson 1976; Trulsson and Essick 1997; Trulsson et al. 1992). Manual handling of the microelectrode was comparable to that employed in dental practice for local anesthesia of the lower teeth. The right or left inferior alveolar nerve or the lingual nerve was approached intraorally with a 0.2-mm-diam tungsten needle electrode. The distal 1 mm of the microelectrode tapered to a 5 μm tip, and the electrode was coated with lacquer to within 10–30 μm of the tip, which provided an impedance of 400–800 kΩ measured in situ at 1 kHz. Neural signals were amplified (×10,000; BW 0.47–5 kHz) by a probe fixed with a headband to one side of the subject’s head.

To guide insertion of the electrode during search for the nerve, electrical stimulation (square-wave pulses of negative polarity, 0.2 ms duration, 0.1–1 mA) was delivered through the electrode. Paresthesias in the tongue or the lower lip indicated that the electrode was close to the nerve. When the nerve-bundle had been impaled, the position of the electrode was carefully adjusted until single afferent impulses could be discriminated. The electrode was then left undisturbed in this recording position, supported only by the surrounding tissue. The single-unit recording was accepted if the spike amplitude was at least twice the background activity, and the unit could be separated by an on-line triggering device (Edin et al. 1988) implemented in the sampling/analysis system (SC/ZOOM, Department of Integrative Medical Biology, Umeå University). Stable single-unit recordings were so obtained for 10–30 min.

**Mechanical stimulation and classification of units**

Nylon filaments (von Frey hairs calibrated at 0.03, 0.06, 0.12, 0.25, 0.5, 1, 2, 4, 8, 16, 32 mN) and blunt glass probes were used for mechanical stimulation of the mucosa of the tongue and lip, facial skin, and teeth. In the tongue, the units were classified as “superficial” and “deep” on the basis of force threshold and receptive field size (see Trulsson and Essick 1997). The superficial units in the tongue, as well as the units in the mucosa of the lip and the facial skin, were further subcategorized using standard criteria and in accordance with the nomenclature suggested for three types of the mechanoreceptors found in the glabrous skin of the human hand: fast adapting type I (FA I), and slowly adapting types I and II units (SA I and SA II) (Johansson et al. 1988a,b; Trulsson and Essick 1997; Vallbo and Johansson 1984). The spatial extent of the receptive field was defined with a von Frey hair at four times the threshold force of the unit, and the receptive field boundary was marked with a fine-pointed ink pen (Johansson and Vallbo 1980). Afferents responding to tooth loads applied by the nylon filaments were classified as periodontal mechanoreceptors (see Trulsson 2006; Trulsson and Johansson 1996). For each unit, the most sensitive tooth to these stimuli was identified. This tooth is referred to as the receptor-bearing tooth (RBT) (Trulsson 1993).

**Microstimulation protocol**

After a stable single-unit recording had been obtained and the unit had been classified according to the criteria described in the preceding text, the electrode was connected to a constant current stimulator delivering positive square-wave electrical pulses, 0.2 ms in duration (Vallbo et al. 1984). Pulse trains at 30 Hz lasting 1.0 s were triggered manually by the experimenter, while stimulus amplitude was slowly increased from zero until the subject reported a sensation during the stimulation period. The subjects were allowed to hear the train of stimulating pulses through a loudspeaker so that they knew when the stimulus was present. Care was taken to keep the stimulus at minimal intensity for a sensation to minimize the risk of exciting several fibers. However, the stimulus intensity often had to be increased successively during a session to continue exciting the afferent, which presumably reflected activity-dependent changes in axonal excitability. A stimulus strength of 10 μA was never exceeded even when a sensation was lacking at this stimulus intensity.

The subject reported the location of the evoked sensation with the aid of a schematic drawing of the face and mouth. The spatial coincidence of the sensation with the receptive field of the unit was verified by a procedure that included alternating electrical stimulation and light mechanical indentation while the subject reported whether the two types of stimulation were felt at the same position (Vallbo et al. 1984). If a matching sensation was reported, the subject was asked to describe its quality as well as the size and shape of the area where it was felt by pointing at various symbols presented on a chart. The subject could also communicate with the experimenter by writing and drawing with a pen on the chart.

Questions and response options offered to the subject included 1) shape of the perceived field? Symbols representing a round, an oval and an irregular field were presented. 2) Size of the perceived field? Symbols representing a “small point,” circular fields with 1–10 mm diameter, and a circular field >10 mm diameter were presented. 3) Sensation continuous within the field or field composed of several points? 4) Superficial or deep? 5) Stationary or migratory? 6) Natural or unnatural? 7) Painful or nonpainful? And 8) sensation best described as tapping, vibration, pressure, other mechanical event, or other kind of sensation? (No distinction was made between a tapping, flutter-like sensation and a hum-like vibration sensation: any type of cyclic mechanical sensation was characterized as vibration).

After the perceptual responses had been characterized with 30 Hz stimulation, the preamplifier was switched back to the recording mode, the unitary integrity of the afferent was confirmed and its properties was reassessed. Units whose recordings were stable after the 30 Hz stimulation were also tested with single pulses and with pulse trains at 5 and 60 Hz lasting 1.0 s. For single pulses, the subjects were simply asked if they could detect the stimulus. For the pulse trains, the subjects were also asked if the sensation was best described as tapping, vibration, pressure, other mechanical event, or other kind of sensation.

**Results**

In total, 35 single mechanoreceptive afferents were isolated and classified, 28 in the inferior alveolar nerve and seven in the lingual nerve (Fig. 1). Of the 28 afferents isolated from the inferior alveolar nerve, 11 responded to loading of teeth in the lower jaw, 8 innervated the facial skin, 4 innervated the vermilion of the lower lip, and 5 innervated the intraoral mucosa of the lower lip. Six of the seven afferents isolated from the lingual nerve innervated the mucosa of the anterior part of the tongue, whereas the remaining afferent was judged to innervate tissues deep down in the muscle mass of the tongue.
Responses of orofacial mechanoreceptors to mechanical stimulation

PERIODONTAL AFFERENTS. Seven of the 11 periodontal afferents responded to loading of more than one tooth, but all showed the strongest responses when one particular tooth was loaded, the RBT. The RBT was the first incisor (I1) for four afferents, the second incisor (I2) for two afferents, the canine (C) for three afferents, and the first and second premolar (P1 and P2) for one afferent each (Fig. 1). All periodontal afferents showed a slowly adapting response to a constant force applied in at least one direction to the RBT. The dynamic response to the onset of the force was fairly weak (peak rates: $<$200 imp/s), and the afferents typically exhibited highly regular responses to constant, maintained tooth loads (Fig. 2A). Six of the afferents were spontaneously active (range among afferents; 6–12 imp/s).

CUTANEOUS AND MUCOSAL AFFERENTS. Both fast and slowly adapting afferents were found in the skin of the face (2 FA I, 2 FA hair, 2 SA I, and 2 SA II), the red zone of the lip (1 FA I, 1 SA I and 2 SA II), and in the mucosa of the lip (3 FA I and 2 SA I; Table 1). For each afferent type, the receptive field characteristics and response properties were similar among the different orofacial tissues. Consistent with previous microneurographic studies of cutaneous afferents, most receptive fields were small circular and oval areas, only a few millimeters in diameter (Fig. 3).

All but two of the fast adapting afferents were classified as FA I afferents and showed burst responses at the beginning and end of a sustained skin indentation. None of the fast adapting afferents was activated by taps applied at sites remote to the receptive fields, indicating that the sample did not include FA II afferents (Pacinian corpuscle afferents) (cf. Johansson and Vallbo 1979; Johansson et al. 1988b). The maximum discharge frequencies obtained in response to rapid skin displacements (the onset or offset of stimulation with the filaments) were ca. 200–300 imp/s. The thresholds as determined with the filaments ranged between 0.06 and 0.5 mN.

Two of the fast adapting afferents in the facial skin showed receptive fields that were limited to a single hair of the beard of one of the subjects. The beard had only been growing for little more than 48 h and was quite short. Even though the response characteristics of the afferents were difficult to determine in detail, it was obvious that the afferents only discharged during movements of the hair and not to maintained pressure by the hair stimulus.

All slowly adapting afferents in the mucosa and red zone of the lip and in the facial skin showed a dynamic response to the onset of mechanical stimuli and a static response to a steady force applied to the receptive field. The maximum discharge frequencies obtained in response to rapid skin displacements were ca. 100–600 imp/s. The SA I afferents were characterized by an irregular static discharge and a high peak discharge rate ($>$600 imp/s). The SA II afferents, on the other hand, typically showed regular static firing, lower peak discharge rates ($<$200 imp/s) and spontaneous activity (Fig. 2B). Three of the four SA II afferents were spontaneously active (range among afferents; 8–14 imp/s).

Two of the slowly adapting afferents to the mucosa and red zone of the lip and in facial skin showed a dynamic response to the onset of mechanical stimuli and a static response to a steady force applied to the receptive field. The maximum discharge frequencies obtained in response to rapid skin displacements were ca. 100–600 imp/s. The SA I afferents were characterized by an irregular static discharge and a high peak discharge rate ($>$600 imp/s). The SA II afferents, on the other hand, typically showed regular static firing, lower peak discharge rates ($<$200 imp/s) and spontaneous activity (Fig. 2B). Three of the four SA II afferents were spontaneously active (range among afferents; 8–14 imp/s).

Table 1. Numbers of mechanoreceptive afferents with terminals in superficial tissues

<table>
<thead>
<tr>
<th>Inferior Alveolar Nerve (n = 17)</th>
<th>Lingual Nerve (n = 6)</th>
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</thead>
<tbody>
<tr>
<td>Facial</td>
<td>Vermilion</td>
</tr>
<tr>
<td>FA I</td>
<td>2</td>
</tr>
<tr>
<td>FA hair</td>
<td>2</td>
</tr>
<tr>
<td>SA I</td>
<td>2</td>
</tr>
<tr>
<td>SA II</td>
<td></td>
</tr>
</tbody>
</table>

FA I, fast adapting type I; SA I and II, slowly adapting types I and II.
AFFERENTS IN THE LINGUAL NERVE. Of the seven afferents isolated from the lingual nerve, six were classified as superficial tongue units innervating the mucosa of the tongue and one as a deep tongue unit innervating the muscle mass of the tongue (Trulsson and Essick 1997). The superficial units showed small circular or oval receptive fields close to the tip of the tongue and responded to low mechanical forces (force threshold range: 0.06–0.5 mN). Four of the superficial units were classified as FA I afferents and two as SA II afferents (Table 1). The FA I afferents responded only during the application and removal of a mechanical stimulus, whereas the SA II afferents showed a dynamic response to the onset of a mechanical stimulus and a static response to a steady force applied to the receptive field. In addition, both SA II afferents were spontaneously active (10 and 11 imp/s). The SA II afferents showed regular interspike intervals both during the spontaneous discharge and during the static response.

The deep tongue unit showed a relatively weak ON response to the application of the mechanical stimuli and a slowly adapting response to probing of a large area of the tongue ($200 \text{ mm}^2$), and it exhibited a high force threshold (8 mN). The afferent was also spontaneously active (16 imp/s; Fig. 2C).

**Sensations evoked by microstimulation of orofacial mechanoreceptors**

Electrical stimulation through the recording microelectrode was pursued with all 35 afferents described above. For each type of afferent described in the preceding text, the sensation evoked by microstimulation was similar among the different types of tissue (e.g., facial skin vs. lingual mucosa). Thus the results regarding the microstimulation will be presented for each afferent type rather than the different tissues innervated by the inferior alveolar and lingual nerves.

**PERIODONTAL, SA II, AND DEEP TONGUE AFFERENTS.** Microstimulation at 30 Hz (18 units) and 60 Hz (6 periodontal afferents) did not elicit a sensation that spatially matched the receptive field with any of the periodontal, the SA II, or the deep tongue afferent. With high stimulus intensities, a remote tactile sensation was usually reported (Vallbo et al. 1984), often located within the mental region. Never was a sensation of tooth movement reported or any other sensation related to the receptor-bearing tooth.

**FA I AND SA I AFFERENTS MICROSTIMULATED WITH PULSE TRAINS AT 30 Hz.** Ten FA I afferents and five SA I afferents were tested with microstimulation at 30 Hz (Table 1). A sensation from eight of the FA I afferents and three of the SA I afferents was generated that matched the location of the receptive field of the afferent. For these 11 afferents, the size of the receptive fields during microstimulation paralleled the size of the receptive fields (Table 2; Spearman’s rho = 0.86; $P < 0.001$), although the former was slightly smaller for both types of units. An accurate correspondence in shape between the perceptive fields and receptive fields was also seen for the majority (9/11) of units (Table 3; Kappa = 0.61, $P < 0.09$; McNemar’s exact test for bias $P > 0.99$).

For all FA I and SA I units, the sensation was evenly distributed within the perceptive field. When the subjects were asked to define whether the sensation was felt superficially or deep, a difference was found between the two unit types in that sensations from FA I units (6/8) were more often superficially located compared with sensations from SA I units (1/3; Table 4). In fact,
TABLE 3. Contingency table demonstrating association between shape of the perceptive field (row value) and shape of the receptive field (column value)

<table>
<thead>
<tr>
<th>Receptive Field Shape</th>
<th>Circular</th>
<th>Oval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perceptive field shape</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oval</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Circular</td>
<td>6</td>
<td>1</td>
</tr>
</tbody>
</table>

When interviewing one subject after the experiment, the subject clearly stated that microstimulation of an SA I unit on the lip felt more like the skin was being pulled down from within rather than pressure being applied to the surface of the skin.

For all type I units, the subjects reported that the sensation at liminal stimulus intensity was stationary and did not move from one point to another within the perceptive field. For two afferents, when the current was increased above the liminal stimulus intensity, a sensation of movement was created. On these occasions, the sensation moved rapidly between the perceptive field of the unit and another point on the lower lip or chin, suggesting that an additional afferent had been excited by the greater current.

When the subjects were asked to rate whether the sensation felt natural or unnatural, a difference was found between the two unit types in that sensations with FA I units (5/8) were more often rated as natural compared with SA I units (1/3; Table 4). Sensations were described as a nonpainful mechanical sensation in all instances. However, a clear difference could be seen between the unit types. The sensation was best described as vibration for all but one of the FA I units. With the exceptional FA I unit, the subject reported a noncyclic pressure. The sensation evoked when stimulating SA I units, on the other hand, was best described as pressure for two of the three units and vibration for the remaining unit (Table 4). It might be significant that the two SA I units that generated a sensation of constant pressure during the 30 Hz stimulation evoked an unnatural sensation located below the surface.

FA I and SA I afferents microstimulated with single pulses and pulse trains at 5 and 60 Hz

After the 30 Hz microstimulation, three FA I afferents and one SA I afferent were tested for microstimulation with single pulses and 1 s pulse trains at 5 and 60 Hz. One stimulus pulse was sufficient for detection with two FA I units. However, the subject had to focus hard to detect the weak sensation and made no attempt to further describe the characteristics of the sensation. All three of the FA I units gave a clear sensation of tapping at 5 Hz stimulation and vibration at 60 Hz stimulation.

Microstimulation of the SA I unit did not evoke any perceptual response with the single pulses or 5 Hz stimulation. However, a clear noncyclic mechanical sensation was reported with 60 Hz stimulation.

Hair afferents

Two FA hair afferents located on the chin of one of the subjects were tested for microstimulation with a 30 Hz stimulus. The two units generated a similar matching perceptual response distinctly related to a single hair. The sensation was described by the subject as a natural, nonpainful mechanical vibration of the single hair. One of the units was also tested with single pulses and pulse trains at 5 Hz. Interestingly, the hair unit showed clear perceptual responses to both types of stimulation. Even though the sensation produced by the single pulses was very weak, it was strong enough to be noticed immediately by the subject. The sensation generated by the 5 Hz stimulation was described as tapping of the hair.

DISCUSSION

The results of the present investigation show for the first time that electrical stimulation of single type I (FA and SA) and FA hair afferents from the orofacial region can evoke a percept that is spatially matched to the afferent’s receptive field. Moreover, the percept is consistent with the afferent’s response properties as observed on natural mechanical stimulation. In contrast to type I and hair afferents, microstimulation of periodontal, SA II, and muscle afferents in the orofacial region failed to evoke a sensation that matched the receptive field of the afferent. Accepting the technical difficulty of recording from and stimulating nerves in the mouth of unanesthetized human subjects, the present material, although small, significantly extend previous findings on single afferent microstimulation, which has been limited to the glabrous skin of the hand.

Response characteristics of orofacial mechanoreceptors to natural stimulation

The first microneurographic recordings from the trigeminal region were reported in 1976 by Johansson and Olsson. However, more than a decade passed before comprehensive accounts of the response properties of orofacial mechanoreceptors were presented (for references, see Trulsson 2006; Trulsson and Johansson 2002).

PERIODONTAL AFFERENTS. All afferents that responded to loading of teeth in the present study were classified as periodontal afferents. These afferents terminate among the collagen fibers in the ligaments that attach the root of the tooth to the alveolar bone (Byers 1985) and provide information about forces applied to the teeth (for reviews, see Trulsson 2006; Trulsson and Johansson 1996). The response properties of the periodontal afferents recorded in the present study were very similar to those described in earlier studies (e.g., Johnsen and Trulsson 2003; Trulsson 1993; Trulsson et al. 1992). First, they exclusively responded to loading of one or more teeth, but all showed the strongest response when one particular tooth was

TABLE 4. Dissimilarity in the qualities of the sensations evoked by microstimulation of FA I and SA I mechanoreceptive afferents

<table>
<thead>
<tr>
<th>Quality of Sensation</th>
<th>Deep</th>
<th>Superficial</th>
<th>Unnatural</th>
<th>Natural</th>
<th>Pressure</th>
<th>Vibration</th>
</tr>
</thead>
<tbody>
<tr>
<td>FA I</td>
<td>2</td>
<td>6</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>SA I</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Contingency table demonstrating association between the depth, naturality, and constancy of the evoked sensation (column values) and type of mechanoreceptive afferent (row value).
loaded in one particular direction. Second, they were often spontaneously active. Third, during loading of the tooth, they typically showed a quite weak dynamic on-response followed by a slowly adapting, highly regular, static response to the maintenance of the load on the tooth.

**CUTANEOUS AND MUCOSAL AFFERENTS.** Consistent with the earlier studies on the facial skin, lips, and oral mucosa, the afferents in the present study demonstrated small circular and oval receptive fields and response properties similar to those of tactile afferents of the human hand, i.e., hair follicle afferents and three types of afferents described in the glabrous skin (SA I, SA II, and FA I afferents). No afferents in the present study showed response properties typical of Pacinian-corpuscle afferents (FA II); this is in agreement with earlier microneurographic studies and psychophysical findings in man (Barlow 1987; Edin et al. 1995; Johansson et al. 1988b).

**HAIR AFFERENTS.** The two hair follicle afferents (FA hair) encountered in the present study appeared to respond exclusively during manipulation of a single hair of the beard of one of the subjects. Similar observations, of hair afferents responding during manipulation of a single mustache hair, have been described during recordings from the infraorbital nerve (Johansson et al. 1988b; Nordin and Hagbarth 1989). In this regard, hair afferents in the trigeminal region differ from those that have been reported in other hairy skin regions of the body. For example, the afferents supplying the hair follicles of the forearm have been reported to innervate >10 hairs evenly distributed over a large area (Valbo et al. 1995).

**DEEP AFFERENTS IN THE LINGUAL VERTE.** One afferent was spontaneously active and showed a slowly adapting response to forceful probing of a large area of the tongue. Consistent with earlier studies, this afferent was classified as a deep tongue afferent, most likely innervating a muscle spindle situated deep in the tongue muscle (Trulsisson and Essick 1997).

**Sensations evoked from microstimulation of orofacial mechanoreceptors**

The present study found that microstimulation of orofacial mechanoreceptors, regardless of the location of the receptive field (facial skin, vermillion, labial or lingual mucosa), led to results that were remarkably similar to those from microstimulation of three of the four classes of mechanoreceptors supplying the glabrous skin of the hand (Macefield et al. 1990; Ochoa and Torebjork 1983; Schady and Torebjork 1983; Valbo et al. 1984). First, of the FA I and SA I mechanoreceptors with sensations projecting to the receptive fields, the size of the receptive field paralleled the size of the receptive field. Moreover, the receptive fields for both body regions tended to be slightly smaller than the receptive fields (Valbo et al. 1984). In addition, for both body regions, there was a general correspondence between the shape of the receptive and receptive fields (Shady and Torebjork 1983; Valbo et al. 1984).

Second, the present study found that the sensations evoked by microstimulation of orofacial FA I mechanoreceptors tended to be located superficially in the skin and were natural in quality and cyclic or vibratory in nature. In contrast, the sensations with SA I afferents tended to be more deeply located in the skin, less natural or unnatural in quality, and often felt as a constant pressure. Similar observations have been reported for microstimulation of mechanoreceptors in the hand nerves with some differences among studies. For example, Vallbo et al. (1984) reported that the sensations evoked in 70% of FA I afferents were natural or almost natural in quality but for only 35% of SA I afferents. Noncyclic skin pulling or pressure sensations have been associated with microstimulation of SA I units. This was found invariably (Ochoa and Torebjork 1983), in a majority (Vallbo et al. 1984), and in 25% of SA I mechanoreceptors tested (Macefield et al. 1990). In contrast, vibratory sensations have been associated with microstimulation of FA I units. This was found invariably (Ochoa and Torebjork 1983), in most (Macefield et al. 1990), and in 50% of FA I mechanoreceptors tested (Valbo et al. 1984).

Third, the present study found that microstimulation of orofacial SA II mechanoreceptors evoked no sensation. Results from studies of SA II mechanoreceptors supplying the hand have yielded identical results. For example, of 17 SA II afferents studied by Ochoa and Torebjork (1983), no sensation was evoked by microstimulation. Similarly, Macefield et al. (1990) found that microstimulation of 83% of 18 SA II afferents evoked no response. Valbo et al. (1984) studied only four SA II afferents. Although sensations were evoked on microstimulation, the authors note that this occurred only on delivery of high currents, suggesting that the sensations were associated with other afferents that had been recruited by the higher currents.

**COMMON FEATURES OF AFFERENTS WITH NO MATCHING SENSATIONS ON MICROSTIMULATION.** The afferents that failed to evoke a sensation during microstimulation (SA II, muscle and periodontal afferents) share several common features. First, they are located at a distance from the surface of the skin/mucosa but in close proximity to supporting structures: muscle afferents terminate in muscle spindles inside a muscle, periodontal afferents terminate in Ruffini-like endings among collagen fibers in the periodontal ligament (Byers et al. 1985), and cutaneous SA II afferents most likely terminate in spindle shaped Ruffini endings located deeply in the dermis (Chambers et al. 1972). Second, they are normally activated by stretching of the supporting structure. Third, they show slowly adapting responses and are often spontaneously active (see Fig. 2). Fourth, they have been shown to provide proprioceptive information of importance for motor control (Edin and Aabbs 1991; Proske 2006; Trulsisson and Johansson 1996). It has been suggested that spatial summation of the activity from many muscle spindle afferents, such as evoked during muscle stretch, is required to ensure synaptic transmission to perceptual levels (Macefield et al. 1990). Indeed the same may be true also for the populations of SA II (Edin and Johansson 1995) and periodontal (Trulsisson 1993; Trulsisson and Johansson 2002) afferents that are activated during natural conditions of stimulation.

Most recently an additional role, one that lay outside the perceptual domain, has been suggested for SA II afferents in close proximity to the nails (Birznieks et al. 2009). It may be that afferents in diverse types of tissues that monitor tension in collagen fibers (e.g., SA-II-type afferents in the dermis, periodontal ligaments, and nail beds) constitute a general proprioceptive system that registers the mechanical state of the soft tissues, thus contributing to the maintenance of the body’s representation in the central somatosensory system. It was
recognized many years ago that the brain requires continuous peripheral afferent input to maintain the body image (Melzack and Bromage 1973). Such activity is indeed provided by the spontaneously active SA II afferents in the facial skin and oral mucosa and by the periodontal afferents surrounding the roots of the teeth.

COMMON FEATURES OF AFFERENTS WITH MATCHING SENSATIONS ON MICROSTIMULATION. Type I units that have superficially located terminals in the skin/mucosa and show small, discrete, receptive fields seem to have a powerful access to the perceptual levels of the somatosensory system. This is particularly true for the FA I afferents often giving a perceptual response even when microstimulated with one single pulse. A particularly large proportion of FA I afferents have been found in the two body areas that serve to manipulate and explore objects, the glabrous skin of the digits and the masticatory mucosa of the anterior tongue (Johansson and Vallbo 1983; Trulsson and Essick 1997). Thus it seems likely that the FA I afferents play a key role in active touch when we use the tips of our fingers and tongue to explore external objects in our environment or our own body, a role that is dependent on a secure and powerful access to the perceptual levels.

Surprisingly, the present results suggest that a similar powerful connection to perceptual levels exist also for hair afferents in the face. Microstimulation with pulse trains evoked a clear perceptual response in the two hair afferents that were studied, and sensations were evoked in one of them also when tested with single pulses. It is plausible that trigeminal afferents innervating hair follicles in the vicinity of the mouth and nose serve a protective function and might have a better access to perceptual levels than hair afferents innervating other areas of the body. Given the large areas of somatosensory cortex devoted to the vibrissae in animals (e.g., cat, rat) that rely on such tactile feedback from the face, it is likely that hair afferents from the face do have a strong access to perceptual levels. However, further microstimulation experiments are needed to clarify this question.

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REFERENCES


