

Proceedings of the Symposium From Osseointegration to Osseoperception: The Functional Translation

PHYSIOLOGICAL CHARACTERISTICS OF LOW-THRESHOLD MECHANORECEPTORS IN JOINTS, MUSCLE AND SKIN IN HUMAN SUBJECTS

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SUMMARY

1. The development of microneurography, in which an insulated tungsten microelectrode is inserted into an accessible peripheral or cranial nerve in awake human subjects, has allowed detailed analyses of the signalling capacities of single mechanoreceptive afferents from the skin, muscles and joints. For example, we know much about how the two classes of rapidly adapting (Meissner and Pacinian) and two classes of slowly adapting (Merkel and Ruffini) cutaneous mechanoreceptors encode forces applied normal or tangential to the skin of the hand and the similarities and differences in glabrous versus non-glabrous skin (and receptors associated with hairs). We also know about stretch- and force-sensitive endings in muscle (the muscle spindle and Golgi tendon organ, respectively) and how they behave during passive or active movements or during isometric contractions. In addition, we have characterized the firing properties of mechanoreceptors in the joint capsules of the fingers. However, we know little about sensory nerves in the periosteum, other than that nociceptors and Pacinian corpuscles exist.

2. In addition to studies on the physiology of sensory endings in human subjects, microstimulation through the recording microelectrode has revealed how the brain deals with the sensory information conveyed by a single afferent. From this work, we know that there is specificity in the sensory channels: electrical stimulation of a single Meissner or Pacinian corpuscle generates frequency dependent illusions of 'flutter' or 'vibration', whereas microstimulation of a single Merkel afferent can produce a percept of 'pressure' and stimulation of a single joint afferent can evoke a sensation of

'joint rotation'. Interestingly, the input from a single Ruffini ending in the skin cannot be perceived and the same is true of muscle spindle afferents. So, where does this leave us with osseoperception from the mouth? Given that the periodontal receptors in the vicinity have been lost, which mechanoreceptive endings could encode forces applied to a bone-implanted prosthesis?

3. Meissner and Merkel endings have very small receptive fields and respond only to local forces. Pacinian corpuscles have an exquisite sensitivity to brisk mechanical events and could respond to such stimuli transmitted through the bone to a remote receptor, but would not be able to encode sustained forces. Ruffini endings also respond to forces applied remote to the receptive field and, unlike the Pacinian corpuscles, respond in a sustained fashion, but would their signals be perceived? Like muscle spindles, it is possible that the coactivation of many Ruffini endings could provide meaningful information. Finally, as we have seen, the input from a single joint receptor can be perceived, but they mostly respond at the limits of joint rotation, so it is unlikely that any associated with the temporomandibular joint could contribute to osseoperception.

Key words: Golgi tendon organs, joint afferents, muscle spindles, osseoperception, tactile afferents.

INTRODUCTION

In 1968, Hagbarth and Vallbo, published a set of papers describing their multi-unit recordings from sensory nerve fibres originating in skin and muscle in awake human subjects, using tungsten microelectrodes inserted through the skin into cutaneous or motor fascicles of peripheral nerves.^{1,2} Over the next 2 years, they published their first reports on the firing properties of single primary afferent axons supplying mechanoreceptors in the skin and muscles.^{3–6} The technique of 'microneurography' was born and has since been applied to detailed analyses of the discharge behaviour of single mechanosensitive endings supplying the face and teeth,^{7–9} as elaborated by Trulsson,¹⁰ and the digital joints,^{11–13} as well as single motor axons supplying skeletal muscles.^{14,15} Although tungsten microelectrodes record preferentially from

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Presented at the Symposium From Osseointegration to Osseoperception: The Functional Translation, Sydney, 16 December 2003. The papers in these proceedings were peer reviewed.

Received 8 August 2004; revision 14 September 2004; accepted 2 October 2004.

large-diameter axons, unitary recordings have also been made from non-myelinated axons (C-fibres) in human peripheral and cranial nerves, both afferent^{16–19} and efferent.^{20,21}

Figure 1 illustrates the principle of microneurography. In this case, a tungsten microelectrode has been inserted into a fascicle of the common peroneal nerve supplying the tibialis anterior muscle, shown schematically in cross-section on the left. In the top record, the microelectrode has impaled the myelin sheath of a spindle primary ending within the tibialis anterior muscle; this ending was spontaneously active at rest and responded with an increase in firing rate during passive plantarflexion of the ankle, which stretches the muscle and, hence, the stretch-receptive ending. In the bottom trace, a microelectrode has encountered a spontaneous post-ganglionic sympathetic axon (C-fibre), firing with the pronounced cardiac rhythmicity (i.e. with the heart beat) typical of a muscle vasoconstrictor neuron. Note that the action potentials generated by the myelinated axon are positive going, whereas those of the C-fibre are negative going. Like recordings from single nerve fibres in experimental animals, all unitary recordings from awake human subjects have strict acceptance criteria regarding their physiological identity.

Our current understanding of human sensory physiology includes the belief that excitation of a particular class of afferent

will generate a particular sensory quality. This concept of sensory specificity has received strong support from the technique of intraneural microstimulation, an extension of microneurography, in which controlled current pulses are delivered through the microelectrode to determine the input–output (stimulus–sensation) function of a single afferent fibre. This approach was first applied to single cutaneous afferents in conscious human subjects by Torebjörk and Ochoa²² and Vallbo²³ in the early 1980s. In practice, the microelectrode is used to locate a single afferent fibre and then to stimulate this intrafascicular site, which allows the experimenter to first identify the afferent and to record its responses to natural stimulation before determining how the brain uses the sensory information evoked by electrical stimulation of this same axon. The validity of the technique relies on there being a stimulus level at which an elementary sensation is projected to a small area of skin in the innervation territory and that this ‘projected field’ and its sensory quality remain constant as the stimulus intensity is increased until a level is reached at which another distinct sensation and projected field are generated.^{12,22–29} The quantal nature of the sensations evoked by intraneural stimulation at higher intensities can be explained by the spread of current to adjacent axons, which, by virtue of the relatively poor somatotopy within nerve fascicles, results in sensory percepts that are referred to sites often remote

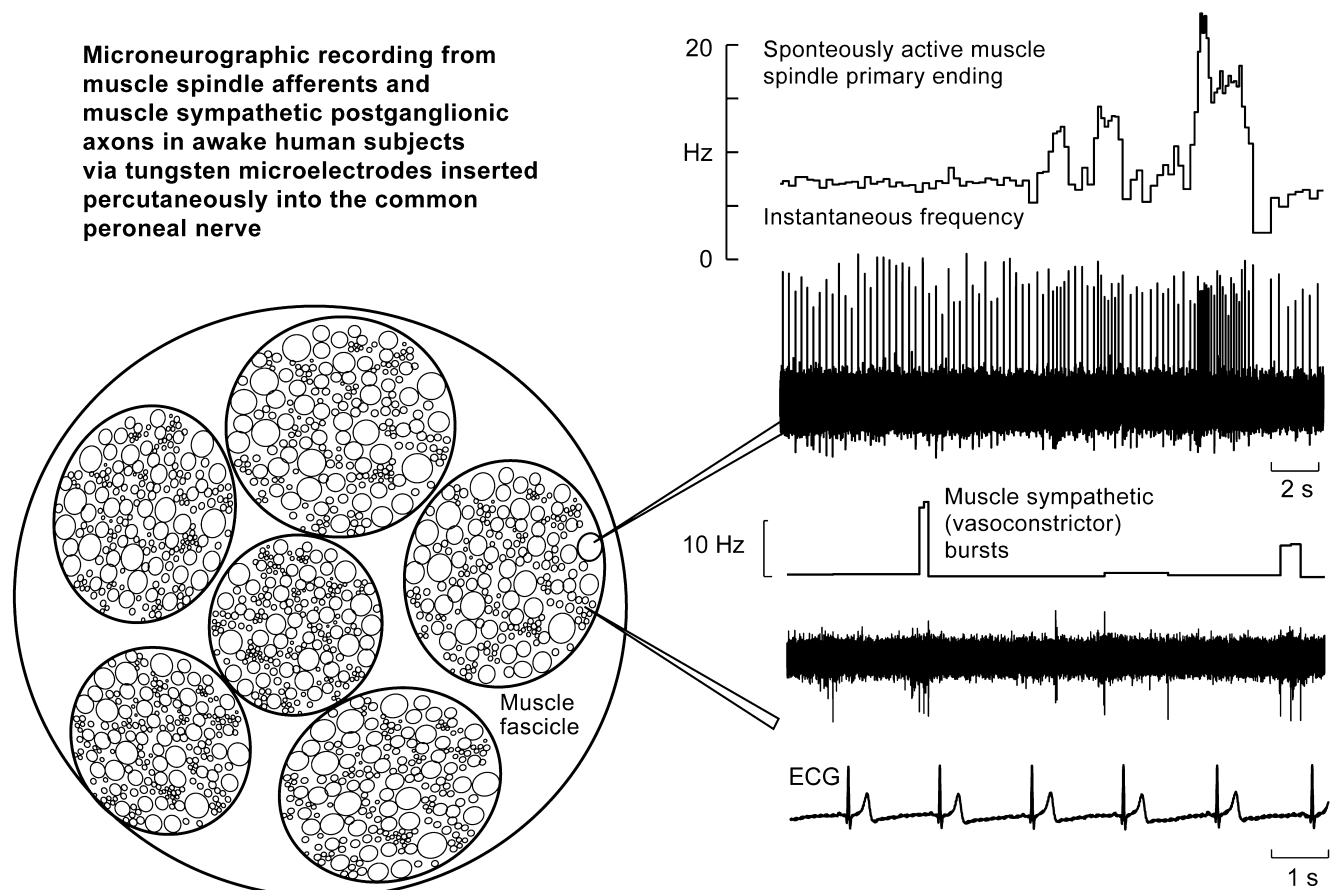


Fig. 1 Schematic representation of a cross-section of a human peripheral nerve. The nerve is composed of distinct bundles of nerve fibres, some innervating muscle (motor fascicles), others supplying skin (cutaneous fascicles). Within each fascicle are large- and small-diameter sensory fibres (afferents) and small-diameter (unmyelinated) post-ganglionic sympathetic fibres. Motor fascicles also contain large-diameter (α) motor axons supplying muscle fibres and (presumed) smaller-diameter (γ) fibres to the muscle spindles. At the top right is an example of a recording from a spontaneously active muscle spindle afferent responding to three imposed stretches of the receptor-bearing muscle. At the bottom right is a unitary recording from a post-ganglionic sympathetic axon and concurrently recorded electrocardiographic activity.

from the receptive field of the afferent that was excited at the lowest stimulus level. The correspondence between an afferent's receptive field and the projected field (as reported by the subject) is remarkably good, supporting the belief that the same sensory axon that can be recorded from the microelectrode is the same axon that is first stimulated electrically.²⁶⁻²⁹

Some of the material presented in this paper has been expanded upon by Rowe *et al.*³⁰ and Trulsson.¹⁰ The present paper will deal only with what is known about the properties of mechanosensitive endings in skin, joint and muscle in human subjects. By understanding how these specialized sensory endings respond to mechanical forces applied to different parts of the body, we will be in a better position to understand how forces applied to osseointegrated implants are transduced into meaningful perceptual information. One cannot doubt the importance of the osseointegration technology, yet one must be cautious in overinterpreting what is meant by the term 'osseoperception'. Indeed, can we perceive forces applied directly to bone or are these forces transmitted to tissues associated with the bone, tissues for which the properties of their mechanosensitive endings are fairly well understood? Although not dealing with receptors in bone *per se*, for which little information is available (other than that bone is well endowed with free nerve endings), the present review will examine whether any of the receptors in tissues associated with bone could respond to forces transmitted through the bone.

MECHANORECEPTORS IN JOINTS AND LIGAMENTS

Because they are located at the interfaces between bones, mechanoreceptors within the joint capsule and ligaments could, conceivably, respond to forces transmitted through the bone. Mechanoreceptors in the posterior capsule of the cat knee joint, identified as Ruffini endings, maintain a sustained discharge to a constant stimulus. They respond in a slowly adapting manner to strains applied in the plane of the tissue, but have very high thresholds to compressive stresses applied perpendicularly;³¹⁻³³ indeed, any responses evoked by compressive forces can be explained by the resultant increases in tensile strain in the immediate receptor environment.³⁴ Ruffini and Golgi-like receptors have also been identified in the human knee joint, as have Pacinian corpuscles.³⁵ Microelectrode recordings from the median and ulnar nerves of awake human subjects have shown that mechanoreceptors associated with the interphalangeal joints and metacarpophalangeal joints, also believed to be Ruffini endings, do not respond to forces applied to bone when there is no movement of the joint and have very high mechanical thresholds to indentation applied over the joint capsule.^{11,12} Although they do respond to joint movements, they respond primarily at the limits of angular excursion. An example of a recording from a human joint receptor is shown in Fig. 2. This unit, located within the metatarsophalangeal joint of the fourth toe, was spontaneously active at rest and responded to extreme plant-

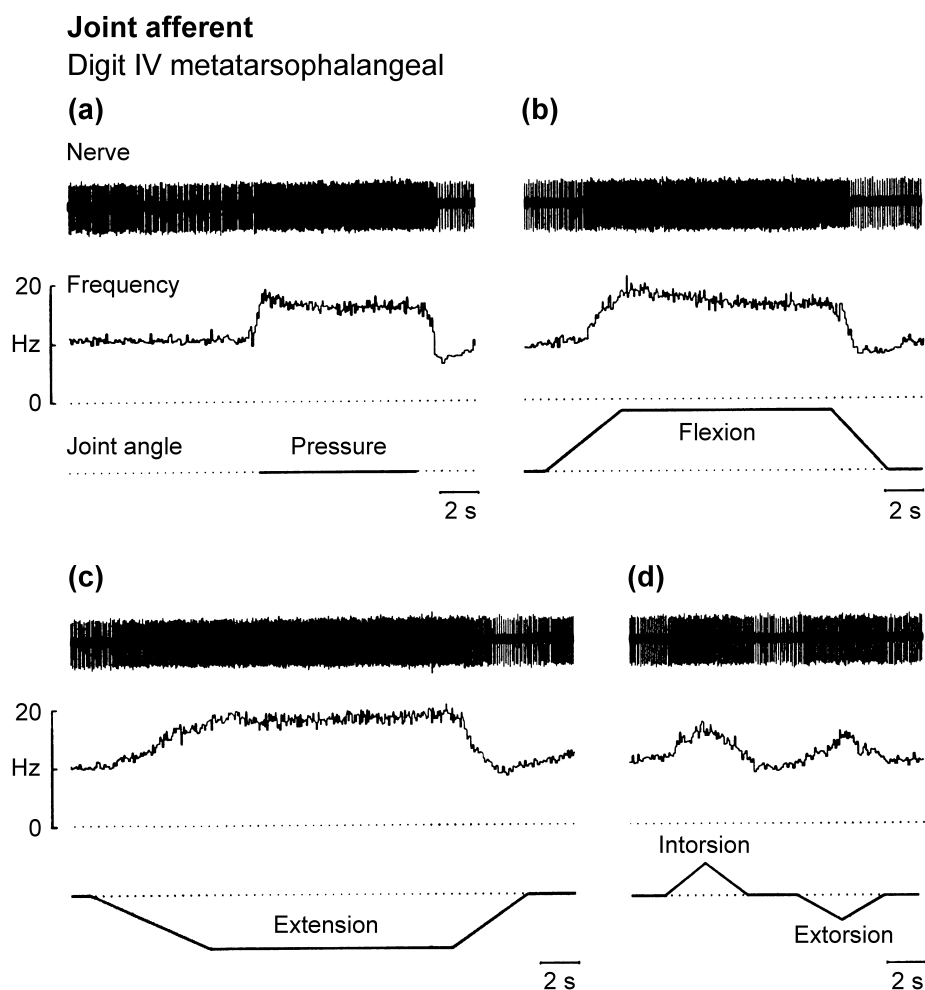


Fig. 2 Unitary recording from a joint afferent associated with the metatarsophalangeal joint of the fourth toe, responding to pressure over its receptive field (a) and to passive flexion (b), extension (c) and longitudinal rotation of the joint (d). Changes in joint angle are represented schematically.

arflexion and dorsiflexion (extension) of the joint. It also responded to rotation of the joint (i.e. imposed (unphysiological) rotation about the longitudinal axis).

Joint afferents often respond in both directions (e.g. flexion and extension) and in more than one axis of rotation (e.g. abduction/adduction and extorsion/intorsion). Accordingly, as a group, joint afferents have a very limited capacity to unambiguously encode forces applied through bone, so it is highly unlikely that these could serve as a substrate for osseoperception. Nevertheless, intraneural microstimulation of a single joint afferent can be perceived as pressure over the joint or as a small movement, so joint afferents do have a strong synaptic coupling to higher-order sensory neurons.¹² This means that, should a joint receptor be exposed to an adequate tensile strain within the joint capsule or extracapsular ligament, it could provide useful information. However, given that these tensile strains are only reached during extreme joint rotations or direct pressure, the reservations on their potential role in osseoperception still stand.

MECHANORECEPTORS IN TENDONS

Tendons insert into bone, so, like joints, receptors in tendons could feasibly play a role in detecting forces conducted through bone. Tendons contain specialized sensory endings, the encapsulated Golgi tendon organs, the long axes of which are orientated in series with the collagenous fibres of the tendon and the muscle fibres to which they are attached. Because of this in-series coupling to muscle fibres, Golgi tendon organs are ideally suited to encode the forces developed by the contracting muscle fibres. However, Golgi tendon organs are notoriously poor at encoding changes in muscle length.^{36,37} As such, these endings do not respond to the longitudinal strains associated with passive joint rotation, but can respond to punctate compressive forces applied directly to the receptive field within the musculotendinous junction or tendon proper. No microstimulation of identified Golgi tendon organ afferents has been performed, so we do not know whether the input from a single afferent can be perceived, but, given their poor sensitivity to the small length changes imparted by vibration of the tendon (at least when the muscles are relaxed³⁸), it is difficult to envisage how these endings could contribute to osseoperception.

MECHANORECEPTORS IN MUSCLES

Muscles contain highly specialized stretch receptors, the muscle spindles, that have been the subject of much investigation. Each muscle spindle comprises several intrafusal ('within the spindle') muscle fibres enclosed within a capsule. There are two types of sensory ending, the primary ending and the secondary ending, both of which adapt slowly to a maintained stretch. Primary muscle spindle afferents, referred to as group Ia fibres, terminate in the annulospiral ending around the central part of the 'bag₁', 'bag₂' and 'chain' intrafusal fibres; secondary muscle spindle endings, referred to as group II fibres, supply the bag₂ and chain fibres.³⁹ Unlike the Golgi tendon organs, muscle spindles are arranged in parallel to the muscle fibres, rendering them incapable of encoding forces generated by the contracting muscle, but very sensitive to length changes within the muscle. Although both primary and secondary endings act as stretch receptors, the primary ending

possesses a higher dynamic sensitivity. Many can be spontaneously active at rest owing to the prevailing degree of passive stretch of the receptor-bearing muscle. Figure 3 shows a recording from one such afferent, which innervated a primary ending in the extensor hallucis longus muscle in the leg, the muscle that lifts (dorsiflexes) the big toe. This ending was spontaneously active at rest and increased its firing during passive plantarflexion of the digit at the metatarsophalangeal joint (represented by the reduction in force measured over the toe), which stretches the muscle and, hence, the spindle. The high dynamic sensitivity of this ending is apparent in the inverse relationship between the force record and the instantaneous frequency seen in Fig. 3a.

Muscle spindles are unique in the somatosensory system in having an efferent innervation: activation of fusimotor (gamma) neurons causes contraction of the intrafusal (but not extrafusal) muscle fibres, thereby recruiting a silent spindle ending, increasing its resting discharge or changing its sensitivity to imposed stretch. This motor innervation shall not be considered further in the present paper, suffice to say that the capacity of muscle spindles to respond to very small length changes is preserved during a voluntary contraction of the receptor-bearing muscle by coactivation of the fusimotor neurons. In the example shown in Fig. 3, the spindle was unloaded (i.e. its firing decreased) during the first two contractions illustrated in Fig. 3b, but this was compensated for during the third, longer contraction in which the unloading was overcome by an apparent increase in fusimotor drive to the intrafusal fibres within this spindle. Muscle spindles respond unidirectionally and with high fidelity to changes in joint angle in one axis throughout the physiological range^{11,12} and the population of muscle spindles distributed throughout the muscles acting on a joint is capable of encoding complex patterns of length changes.^{40,41} These receptors can be exquisitely sensitive, responding to rather light tapping, vibration or pressure applied to the skin overlying the receptive field within the muscle belly, and respond to brisk mechanical events transmitted through the tendon, as well as to sustained forces applied to the tendon. Muscle spindles are very sensitive to vibration of the muscle belly or tendon, responding to a wide range of frequencies:⁴² the spindle illustrated in Fig. 3 even responded to vibration over the nail of the big toe!

Muscle spindles are the sensory endings primarily responsible for our proprioceptive acuity: small-amplitude vibration applied to muscles or tendons was the first convincing demonstration that these intramuscular stretch receptors contribute to proprioception.⁴³ Subsequent studies showed that pulling or vibrating surgically exposed tendons in awake subjects evoked illusions of joint movements⁴⁴ and such illusory movements could also be produced by intraneural electrical stimulation within muscle fascicles of peripheral nerves.⁴⁵ However, microstimulation of a single muscle spindle afferent is not perceived by the subject; apparently, the synaptic strength between spindle afferents and higher-order neurons is so weak that coactivation of many spindle afferents is required to generate perceptual responses.¹² A limiting factor in the potential contribution of muscle spindles to osseoperception is that, unless adequate changes in tendon and, hence, muscle length occur, muscle spindles will not respond. Nevertheless, if bone-conducted forces are sufficient to cause small changes in muscle length, then the spindles located remote to the site of mechanical stimulation may respond.

MECHANORECEPTORS IN THE SKIN

The skin contains many specialized mechanosensitive endings that subserve the broad sense of 'touch' and also contribute to

proprioception and motor control. The majority of human micro-neurography studies have characterized the physiology of tactile afferents in the glabrous skin of the hand, but mechanoreceptors in the hairy skin of the hand, forearm, leg and face have also been

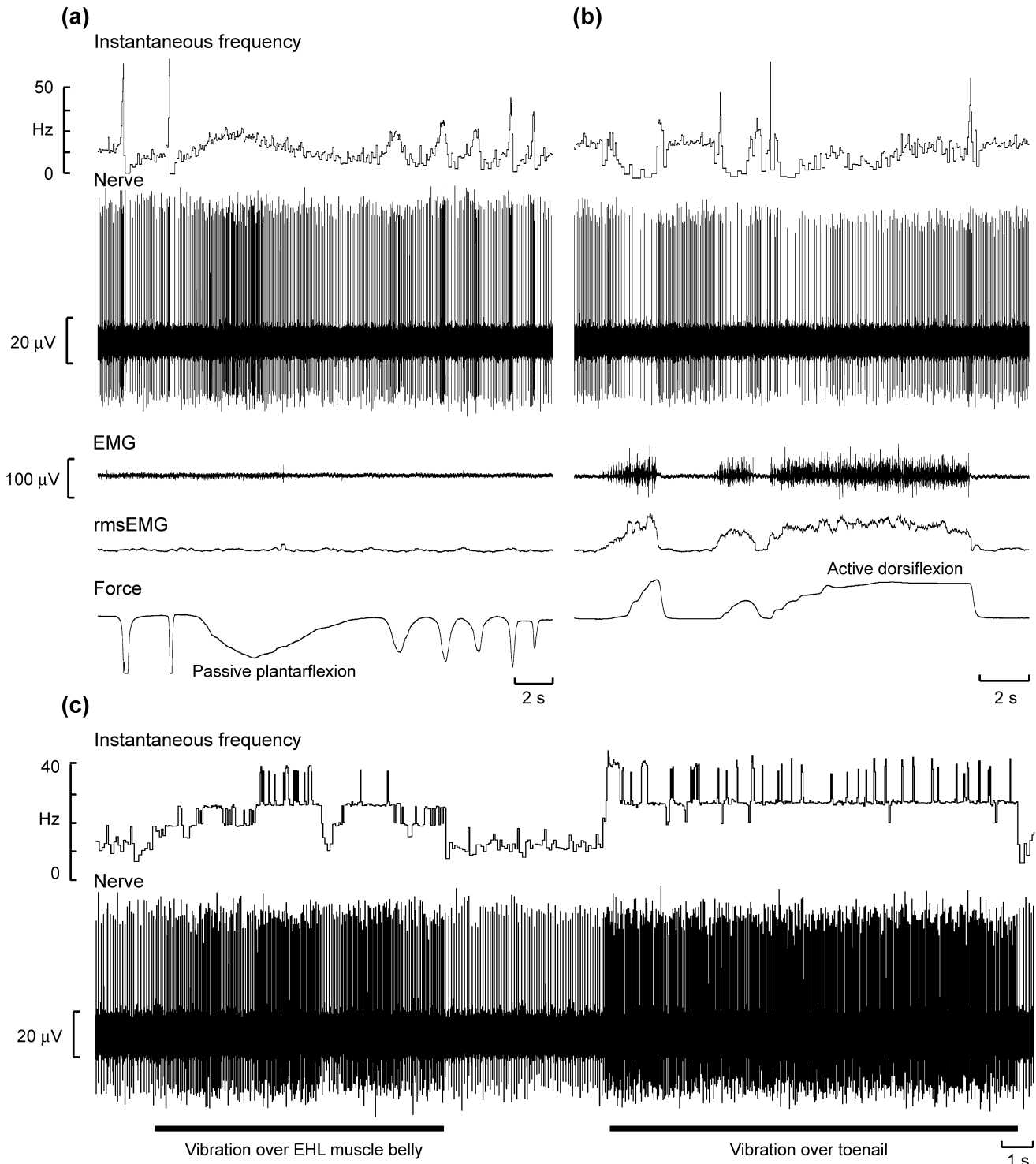


Fig. 3 Unitary recording from a spontaneously active muscle spindle primary ending located in the extensor hallucis longus (EHL) muscle. The afferent increased its firing during stretch of the receptor-bearing muscle induced by passive plantar flexion of the digit at the metatarsophalangeal joint (a). During a weak voluntary contraction, the spindle was unloaded during the first two contractions but overcame this unloading during the third contraction (b). The spindle responded to vibration (approximately 90 Hz) applied via a hand-held stimulator over the receptive field within the muscle belly, as well as over the toenail; the latter indicates that the vibratory stimulus was transmitted adequately through the digit and, via the tendon, to the muscle (c). EMG, electromyographic activity recorded via surface electrodes over the EHL muscle; rmsEMG, root mean square-processed EMG.

examined. Microelectrode recordings from the median and ulnar nerves in human subjects have revealed the existence of four classes of low-threshold mechanosensitive afferent supplying the glabrous skin of the hand, which correspond to the four types of specialized sensory endings identified histologically:⁴⁶ Meissner and Pacinian corpuscles, Merkel cell–neurite complexes and Ruffini endings. The structure of each type of ending confers on it different mechanical filtering characteristics. For instance, the multilamellated Pacinian corpuscle prevents the transduction of slow mechanical events: only brisk mechanical transients can penetrate to the generator region of the terminal. Two classes of afferent adapt rapidly to a sustained indentation of the skin ('fast-adapting'), types FAI and FAII, and two classes of afferent maintain their firing throughout the stimulus ('slowly adapting'), SAI and SAII. Based on behavioural similarities with afferents recorded in the cat and monkey,⁴⁷ it is believed that the FAI and FAII afferents supply the Meissner and Pacinian corpuscles, respectively, and the SAI and SAII afferents supply the Merkel cell–neurite complex and Ruffini ending, respectively.⁴⁸ Type I tactile afferents have small circular or ovoid receptive fields with distinct borders, each receptive field encompassing several small zones of maximal sensitivity ('hot-spots') that represent the individual Meissner corpuscles supplied by a single FAI afferent and the Merkel cell–neurite complexes innervated by each SAI axon.^{48,49} The type II afferents have a single zone of high sensitivity and large, poorly defined borders.

Fast-adapting type I (Meissner) afferents can only be activated by discrete stimuli in a small, well-defined area. They are particularly sensitive to light stroking across the skin, responding to local shear forces and incipient or overt slips within the receptive field. Although they have a very high dynamic sensitivity, they do not respond to vibratory stimuli outside their receptive field: they

do not respond to mechanical transients transmitted through bone. The FAII (Pacinian) afferents are exquisitely sensitive to brisk mechanical transients. Unlike the FAI afferents, FAII afferents respond vigorously to blowing over the receptive field, responding to the fricative quality of the airflow generated by the experimenter blowing through pursed lips onto the receptive field area (they do not respond when blowing through a straw, for example). This is illustrated in Fig. 4. Characteristically, FAII afferents can be stimulated by tapping over areas remote from the site of maximal mechanosensitivity: a Pacinian corpuscle located in a digit will usually respond to tapping the table supporting the arm or tapping the arm itself, as shown in Fig. 4.

This capacity to respond to brisk (but not slow) tissue-conducted mechanical stimuli makes FAII afferents a prime candidate in contributing to osseoperception. However, it should be emphasised that these endings usually respond only with only spike to a mechanical transient; they do not respond to a sustained, non-vibratory stimulus, but will follow vibration frequencies exceeding 400 Hz.

Slowly adapting type I afferents (Merkel) characteristically have a high dynamic sensitivity to indentation stimuli applied to a discrete area and often respond with an off-discharge during release. Although the SAII afferents do respond to forces applied normal to the skin, a unique feature of the SAII afferents is their capacity to respond also to lateral skin stretch. Many possess directional sensitivity, the discharge of some afferents increasing with stimuli applied in certain directions, but decreasing in others.^{4,48,50} A small proportion of SAII afferents are spontaneously active at rest, presenting a characteristically regular discharge.

Five classes of myelinated tactile afferent have been recorded from the lateral antebrachial cutaneous nerve, which supplies the hairy skin of the human forearm: two types of slowly adapting

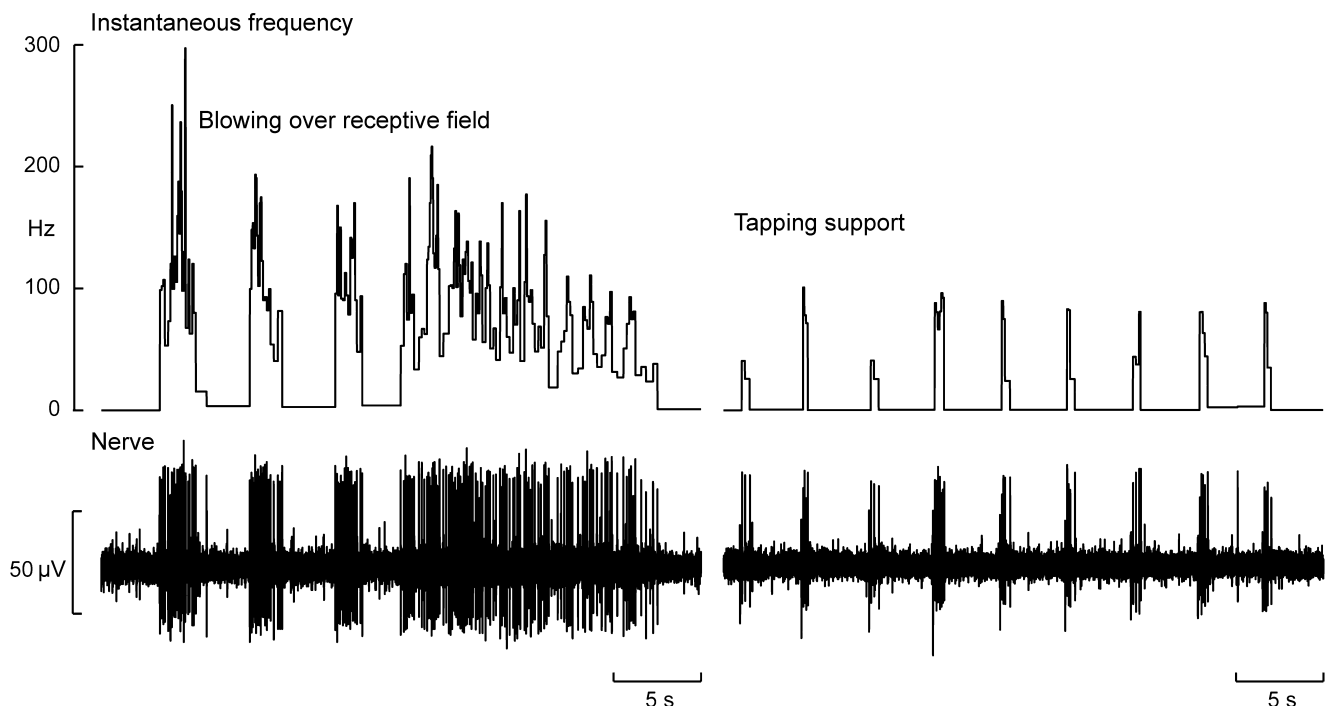


Fig. 4 Unitary recording from a 'fast-adapting' type II (FAII) cutaneous afferent (Pacinian) located in the proximal phalanx of the index finger to blowing over the receptive field and to tapping the supporting table.

afferent (SAI and SAIL) that can be classified in a similar fashion to those in the glabrous skin and three types of rapidly adapting afferent (hair units, field units and Pacinian units).⁵¹ Hair units respond specifically to movements of individual hairs and air puffs onto the receptive field, whereas field units respond to actual skin contact. Hair units in the forearm have large ovoid or irregular receptive fields composed of multiple sensitive spots that corresponded to individual hairs. On average, each afferent supplies 20 hairs.⁵¹ The field units show a similar arrangement of multiple high-sensitivity spots^{11–13} making up a similarly large area, although the individual spots are larger and less isolated than those of the hair units. Microelectrode recordings from the infra-orbital nerve have shown that the hairy skin of the human face is innervated by rapidly adapting and slowly adapting afferents with properties identical to those of the FAI and SAI afferents found in

the hand.⁴⁸ A distinct population of slowly adapting afferents that present a very regular discharge characteristic of SAIL endings has also been found, although their responsiveness to skin stretch could not be tested. Interestingly, no FAII afferents were encountered; this suggests an absence of Pacinian corpuscles in the human face^{7,8} and fits with the low sensitivity of the face to high-frequency vibration.⁵² Mechanical thresholds of afferents on the face are similar to those in the glabrous skin.^{8,53}

Unlike glabrous skin, the hairy skin is only loosely connected to the subcutaneous tissues, thereby allowing greater stretch and, hence, greater activation of stretch-sensitive cutaneous afferents.^{53–55} There do appear to be significant differences in the movement sensitivity of tactile afferents in the non-glabrous and glabrous skin. For instance, 92% of the afferents on the dorsum of the hand responded to finger movements,⁵³ whereas only 68% of

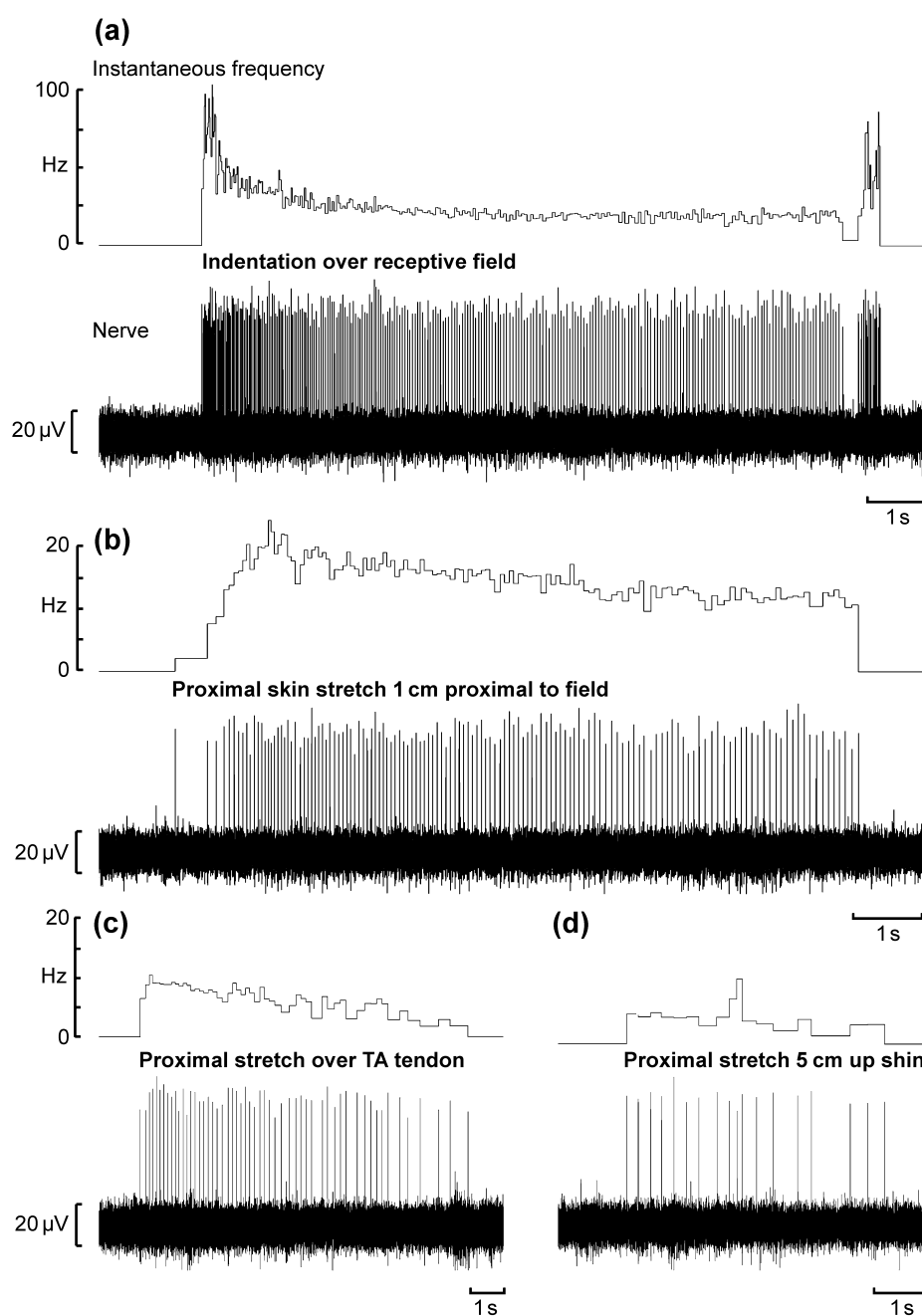


Fig. 5 Unitary recording from a 'slowly adapting' type I (SAI) cutaneous afferent (Merkel) to indentation over the receptive field (a) and to proximal stretch of the skin at progressively more remote locations (b–d).

afferents on the palmar side of the hand responded to passive finger movements¹¹ and 77% responded to active movements.⁵⁶ Moreover, unlike afferents from the glabrous skin of the hand, the majority of afferents on the dorsum respond throughout the physiological range of joint rotation, increasing their firing rate as the skin is stretched during flexion of the digital joints. The FAI afferents respond only to movements of the joint over which they are located, but both the SAI as well as SAI afferents are very sensitive to the skin stretch associated with finger movements, whether this is produced by rotation of the nearest joint or by movements of remote digital joints. The static sensitivity to stretch is high for both classes of slowly adapting afferent:⁵⁴ when measured at an equivalent joint angle, the static sensitivity of the SAI and SAI afferents is similar to that of muscle spindle endings in the long extensors of the fingers, 0.2–0.5 Hz per degree of rotation of the metacarpophalangeal joint.^{37,54} Figure 5 shows the behaviour of an SAI afferent recorded from the common peroneal nerve, cutaneous fascicles of which innervate the hairy skin on the dorsum of the foot and the lateral aspect of the leg. Like all SAI afferents, this unit had a well-defined receptive field, encompassing a 2–3 mm oval of skin between the first and second toes. It responded in a slowly adapting fashion to punctate stimuli applied within its receptive field, but also responded to skin stretch applied remote to the receptive field. Indeed, this receptor responded to skin stretch applied 5 cm proximal to the ankle, some 25 cm away! Recently, Edin⁵⁷ has shown that there may be a third type of slowly adapting receptor in hairy skin; the so-called SAIII was found in recordings from the lateral cutaneous femoral nerve, which supplies the anterior thigh and knee area and possesses properties intermediate between the SAI and SAI afferent types. Like these two classes, the SAIII exhibits a high static and dynamic sensitivity to skin stretch, responding with high fidelity to movements of the knee joint.

Like other hairy skin sites, the hairy skin of the face is also well equipped with receptors for measuring movements of the skin: both rapidly and slowly adapting cutaneous afferents recorded from the infra-orbital nerve^{7,8} respond well to movements of the facial skin associated with phonation and mastication, which supports their provision of proprioceptive information during orofacial movements.^{7,8}

Three independent research groups have shown that stimulation of single FAI, FAII and SAI afferents innervating the glabrous skin of the hand evoke elementary sensations of a specific quality.^{12,22–29} A single pulse delivered to a single FAI afferent can be detected if the subject's attention is directed to it, whereas an SAI afferent requires more impulses and greater attention.²⁸ This also fits with the lower mechanical threshold of FAI afferents and confirms an earlier interpretation of psychophysical thresholds that subjects can detect a single impulse generated by a single FAI receptor.⁵⁸ Stimulating a single FAI afferent with a low-frequency train generates a percept of intermittent tapping that, as the frequency of stimulation increases, becomes one of flutter or vibration; stimulation of a single FAII afferent with a train of pulses always generates a frequency dependent perception of mechanical vibration. Percepts of sustained pressure can be evoked by selective stimulation of SAI afferents, the magnitude of which increases with increasing stimulation frequency, although, as noted above, the generation of a sensation by this class of afferent does appear to be more dependent on the subject's attentional state. Nevertheless, the impulse codes used by rapidly and slowly adapting tactile afferents

are quite distinct: increasing frequency of stimulation signalling increasing vibration with the former and increasing pressure with the latter. Stimulation of a single SAI afferent with a train of pulses usually does not elicit a sensation, although there is evidence that some SAI afferents located near the nailbeds may be able to provide meaningful sensations of joint movement.¹²

CONCLUDING REMARKS

Although little is known about receptors in bone in human subjects, there are many mechanoreceptors in the tissues around and over the bone to warrant caution in attributing 'osseoperception' to receptors in the bone itself. If applied forces cause bone movement, it is clear there will be negligible activation of receptors in the joints and ligaments, which respond primarily at the limits of joint excursion. The same is true of receptors within tendons, which respond only when tensions are high, as in a muscle contraction, but not during passive stretch. However, sufficient bone movement may stretch the tendon and activate muscle spindles, which are very sensitive to small movements. Small movements may also be sensed by specialized mechanoreceptors in the skin overlying the bone: FAII (Pacinian) and SAI (Ruffini) afferents can respond to stimuli applied remotely to their receptive field, as can SAI (Merkel) afferents in the more mobile hairy skin. The other types of cutaneous mechanoreceptor respond to stimuli applied only within their small receptive fields. Of the cutaneous receptors, the Pacinian corpuscles are the most sensitive to distant stimuli and respond to brisk (but not slow) mechanical transients conducted through bone and other tissues but, given their lack of static sensitivity, could not provide information on sustained force. Moreover, their apparent absence in the skin of the face would limit their involvement in bone-conducted stimuli from the mouth.

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