



Review

Oral somatosensory awareness

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ABSTRACT

Oral somatosensory awareness refers to the somatic sensations arising within the mouth, and to the information these sensations provide about the state and structure of the mouth itself, and objects in the mouth. Because the oral tissues have a strong somatosensory innervation, they are the locus of some of our most intense and vivid bodily experiences. The salient pain of toothache, or the habit of running one's tongue over one's teeth when someone mentions "dentist", provide two very different indications of the power of oral somatosensory awareness in human experience and behaviour. This paper aims to review the origins and structure of oral somatosensory awareness, focussing on quantitative, mechanistic studies in humans. We first extend a model of levels of bodily awareness to the specific case of the mouth. We then briefly summarise the sensory innervation of oral tissues, and their projections in the brain. We next describe how these peripheral inputs give rise to perceptions of objects in the mouth, such as foods, liquids and oral devices, and also of the mouth tissues themselves. Finally, we consider the concept of a conscious mouth image, and the somatosensory basis of "mouth feel". The theoretical framework outlined in this paper is intended to facilitate scientific studies of this important site of human experience.

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1. Introduction

The mouth has a special status within the somatosensory system. First, it is one of the most densely innervated parts of the body, in terms of peripheral receptors. This sensory richness is linked to the key role of oral sensorimotor control in eating, drinking, and speaking, as well as to the vivid nature of many oral sensations. Second, the mouth contains a large range of different tissue types (skin, muscle, teeth) in close proximity and constant interaction. These generate very rich patterns of somatosensory afferent input. Third, being a cavity, it has some somatosensory properties typical of the external surfaces of the body, and others more characteristic of the internal milieu. Thus, oral sensations provide an important interface experience, of both the objects in the mouth, and of the states and movements of the mouth itself. Nevertheless, oral somatosensation remains relatively little understood. For example, the research literature on oral somatosensation is sparse compared to that on manual somatosensation, despite similarly rich somatosensory supply.

Moreover, very few studies have considered the sensations and processes specific to the mouth, and their functional significance. For example, visual experience of the inside of the mouth is rare, and is largely confined to occasional and deliberate self-inspection of one's mouth in a mirror. This makes an important contrast with the functions of the hand, which are often visually-guided. The somatosensory innervation of the hand, although very rich, normally remains subservient to vision (Hartcher-O'Brien et al., 2008; but see Tipper et al., 2001; Van Beers et al., 2002). In contrast, within the mouth, somatosensation rules. A second specificity of oral somatosensory function comes from self-touch. Contact between different surfaces in the mouth, such as tongue and palate, or upper and lower teeth is rich and constant. This means that we often, perhaps always, have somatosensory experience of the mouth itself as an object of perception sensed by other oral tissues. Often, these sensory inputs are generated by the active movement of oral tissues, and are subject to gating or attenuation (Blakemore et al., 2000). For example, some rabbit trigeminal sensory neurons receiving from periodontal ligament receptors showed phasic reduction of excitability just before and during the occlusal phase of mastication, suggesting that the centres that generate oral motor commands also selectively modulate sensory transmission. However, these reductions were neither total, nor universal, since high-threshold mechanoreceptors showed an increased excitability during occlusion, consistent with their potential role in detecting damaging levels of force (Olsson et al., 1986).

The prevalence of self-touch in the mouth may explain the perceptual salience of any structural change in the mouth, such as a new filling, or the gap left by extraction of a tooth. In contrast, self-touch in the somatic sensory system is largely restricted to a set of deliberate activities such as scratching, stroking and grooming, so the experience of self-touch is much more limited. The hand, like the mouth, is an important source of specific afferent sensations, but the awareness of the hand as a perceptual object in itself, seems limited (Longo and Haggard, 2010) compared to the mouth. We speculate that near-continuous self-touch of oral, but not manual tissues, may underlie this difference.

In this paper, we introduce and review the concept of oral somatosensory awareness. We first briefly summarise the sensory innervation of oral tissues, and their projections in the brain. We next aim to show how these peripheral inputs give rise to perceptions of objects in the mouth, such as foods, liquids and oral devices. Finally, we consider the somatosensory basis of "mouth feel", and the concept of a conscious mouth image. Our review is positional rather than systematic: we aim to integrate neurophysiological and psychophysical data in support of a specific theoretical model of

oral somatosensory awareness. To do this, we primarily review quantitative, mechanistic studies in humans and primates. We also focus on studies inside the oral cavity, rather than on perioral tissue, and we focus on studies published in the last 20 years. For more exhaustive reviews of specific sub fields, the reader may wish to consult other reviews, such as Trullsson and Johansson (2002) for human neurophysiology, Sakamoto et al. (2010) for somatosensory processing of the tongue in humans, Sessle (2006) for a review of oral sensorimotor processes and their clinical relevance in humans and Kaas et al. (2006) for somatosensory cortical studies of oral representation in primates.

2. A theoretical model of oral somatosensory awareness

Fig. 1 shows a simple model of somatosensory perception (Longo et al., 2010), adapted for the specific case of the mouth. The model presents a hierarchy of three stages of sensory processing, reflecting identified levels in the somatosensory pathway. The first level is *somatosensation* proper. This refers to the awareness of individual afferent events, such as touches, noxious stimuli, etc. Studies of the ability to detect electric shocks applied to the skin, or directly to the nerve (Dong et al., 1993; Fried et al., 2011; Robertson et al., 2003; Trullsson and Essick, 1997) measure this level of awareness. The second level, which we call *somatoception*, refers to the processing of several sensory inputs to form a percept of a specific object or stimulus source. A crucial feature of this level is the integration and combination of information from different receptor types, and different regions of the receptor surface. For example, if I squeeze a peach between finger and thumb to tell if is ripe, my brain must integrate force, position and tactile signals from both digits, to form a somatosensory percept of the fruit. An almost identical process occurs in oral somatosensation, for example when testing whether pasta is cooked *al dente*. An interesting variant of somatoception occurs in self-touch. Here, the object being perceived is another part of one's own body. For example, one can explore the teeth with the tongue in order to perceive a newly-chipped tooth, or the asperity of a filling.

The third and final level of the somatosensory hierarchy is *somatorepresentation*. This refers to the representation of the body as an object in itself. Through continued somatosensory and other inputs, we gradually build a representation of what our body is like, i.e., a conscious image of the body as a physical object. Importantly, this representation cannot be generated directly by any single somatosensory afferent signal. For example, no somatosensory receptors can signal the size of individual body parts, yet we are able to judge the lengths of individual fingers, albeit with some distortion (Longo and Haggard, 2010). Rather, this information is somehow extracted and abstracted from several repeated sensory experiences involving the relevant body parts. Thus, somatorepresentations provide a stored reference model of what one's body is like *in general*, and independent of its current sensory state. For example, the somatorepresentational level may specify that the fingers are attached to the hand, which is attached to the arm, or that the tongue is interposed between the palate and the lower jaw. Two sources of information may be particularly important in specifying these physical facts about the body. First, *vision* of one's own body provides precise information about the shape and size of some body parts. Second, *self-touch* between body parts allows somatosensory input from one part to build up perceptual information contributing to a somatorepresentation of another body part. In the case of the mouth, vision probably plays a minimal role. In contrast, self-touch plays a dominant role in generating the 'conscious mouth image'. This represents an interesting inversion of the case for the hand and other body parts, where vision may play a major role, and somatosensory information is relatively weak. This difference

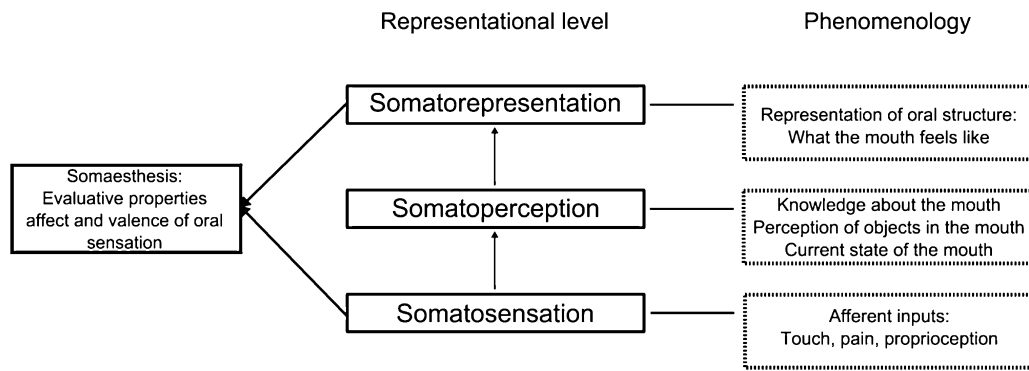


Fig. 1. Three levels of somatosensory representation. See text for details.

may explain why the stored ‘semantic’ representation (Schwoebel and Coslett, 2005) of the mouth is relatively poor. While we are not aware of formal studies on this point, we suspect that fewer people know how many teeth they have than know how many fingers they have.

The three processing stages of the theoretical model shown in Fig. 1 can be related to different stages of the oral somatosensory pathway. Therefore, the bulk of this review is structured according to a hierarchical perceptual model of oral somatosensory awareness. First, we describe the sensory innervations of the oral tissues, and the different classes of peripheral receptor that give rise to them. Second, we describe the core projections of the afferent signals from these receptors to the cerebral cortex. This section covers the processes of somatosensation, and primary conscious experience of oral stimuli. Third, we describe the perceptual functions of the oral somatosensory pathway, corresponding to the somatoperceptual level. We cover both perception of external objects, and perception of the mouth as an object in itself, through self-touch. Fourth, we will review the relatively sparse literature on the conscious mouth image. We suggest that the conscious mouth image can be equated with oral somatorepresentation, and the stored knowledge of one’s own mouth structures. Finally, we end with a description of the neural basis of oral affective sensation, and the basis of pleasant or unpleasant “mouth feel”. Throughout, we focus on the somatosensory rather than chemosensory modalities: we discuss touch, and to some extent pain, but we do not aim to cover taste.

3. Somatosensory oral innervation

The oral tissues are among the most richly innervated of any in the human body, in terms of the number and variety of receptors that they contain. These receptors send afferent signals to the brain, signalling mechanical events (touch), thermal events (heat, cold, warmth), and noxious events (pain). The signals can be subdivided in different ways, according to the specific tissues of origin, the type of receptors, the anatomical characteristics of the afferent fibres, or the quality of the resulting sensation. However these different classifications strongly overlap, because the oral somatosensory system has a characteristic ‘labelled line’ organisation (Müller, 1843). As a broad generalisation, each type of receptor produces a characteristic sensation. Therefore, we have chosen to present the wide range of oral somatosensory signals by describing the different receptors and their locations in the oral tissue.

3.1. Innervation of the oral cavity, and afferents from the mouth

The oral sensory receptors that project to the brain via the trigeminal nerve are summarised in Table 1. The physical events

transduced by these different classes of receptors must be conveyed to the brain in order to produce conscious sensation. The main sensory nerve innervating the orofacial area is the trigeminal nerve. It is a mixed nerve containing both sensory and motor fibres. The sensory nerve endings innervate the teeth, tongue, oral mucosa, masticatory muscles and facial skin.

3.1.1. Mechanoreceptors

Mechanoreceptors convey information regarding a range of mechanical sensory events, including touch, pressure, vibration and proprioception (Dong et al., 1993; Nordin and Hagbarth, 1989; Trulsson and Johansson, 2002). Different types of mechanoreceptors innervate a wide range of oral tissues, including the tongue, the periodontal ligament, the gingiva and the palate (Jacobs et al., 2002). Mechanoreceptors can be classified according to their morphology (e.g., Merkel discs, free nerve endings or Ruffini endings). These different receptor types are associated with different responses of afferent fibres to continuous stimulation. Slowly adapting (SA) fibres show a persistent discharge in response to a static mechanical stimulus. Rapidly adapting (RA) fibres show only an initial response at stimulus onset. Finally, the activation of different fibre types produces different qualities of tactile sensations, such as light touch, flutter, sustained pressure (Capra, 1995). Sensory abilities vary greatly and systematically across the facial and oral structures (Posnick et al., 1990). This variation is ascribed to differences in the density of sensory afferent endings in different tissues. The perioral and midline structures generally have high mechanoreceptor innervation density (Trulsson and Johansson, 2002), and correspondingly lower thresholds for two-point tactile discrimination (Ringel and Ewanowski, 1965).

Turning to specific oral structures, the tongue is innervated by different types of mechanoreceptors, found at both a deep and a superficial level. The superficial mechanoreceptors are mostly fast-adapting. This highly sensitive area may form a kind of oral fovea, comparable to the innervation of the finger tips. The sensory surface of the tongue is often thought to have a specific role in haptic exploration and exteroceptive tactile perception of objects in the mouth. In addition, it plays an important role in *self-touch*, as when the tongue is actively moved into contact with other oral tissues in a process of sensory exploration. Mechanoreceptors located more deeply within the tongue muscle have higher response thresholds and are mostly slowly adapting. They are reliably active during tongue movements in absence of contact with the receptive field on the tongue (Trulsson and Essick, 1997). They therefore convey information that is more proprioceptive rather than tactile in nature. Finally, the distribution of mechanoreceptors across the tongue is not even. The anterior parts of the tongue are more sensitive compared to posterior parts, and the middle part is more sensitive than the lateral parts (Trulsson and Essick, 1997). Thus,

Table 1
The principal somatosensory receptors innervating oral tissues. Note that the presence of Pacinian-like receptors in the tooth pulp is controversial. Illustrative references are given.

Receptor type	Stimulus type	Afferent fibre type	Receptor morphology	Present in oral cavity	Distribution within oral tissues
Mechanoreceptor	Touch	A β (also some C)	Merkel cells (slowly adapting type I)	Yes	All soft tissues in the mouth, including the mucosa (Bukowska et al., 2010; Trulsson and Essick, 2010) and lips (Nordin and Hagbarth, 1989)
			Ruffini endings (slowly adapting type II)	Yes	All soft tissues in the mouth, especially the PDLM, tongue, and mucosa (Dong et al., 1993; Trulsson and Essick, 2010)
			Meissner corpuscles (rapidly adapting type I)	Yes	All soft tissues in the mouth, for mucosa see Trulsson and Essick (2010)
			Pacinian corpuscles (rapidly adapting type II)	Yes	Pacinian-like receptors may exist in the dental pulp (Dong et al., 1993; but see also Byers and Närhi, 1999)
Nociceptor	Pain temperature	A δ	Free nerve endings (rapidly adapting)	Yes	All soft tissues in the mouth, including PDLM (Dong et al., 1993), gingiva, tongue, palate, mucosa (Byers and Närhi, 1999; Pigg et al., 2011). Nociceptors are also found in the tooth pulp and dentine (Byers and Närhi, 1999), where they may be the only type of sensory receptor present
		C	Free nerve endings (rapidly and slowly adapting)	Yes	

the sensory innervation of the tongue involves a form of tactile fovea.

The periodontal ligament attaches the tooth to the bones of the upper or lower jaw. It is also innervated by mechanoreceptors, which project to the brainstem via the trigeminal ganglion. These respond to stimuli applied to the tooth that the ligament supports. The primary function of these receptors appears to be in regulating the forces applied by the teeth in occlusion, mastication, and biting (Türker et al., 2007). Microneurographic studies showed that the firing rates of these receptors strongly varied with the direction of force applied to the tooth, and showed greater sensitivity at low force levels (Trulsson, 2006). The response at low force levels could be important for delicate manipulation of food within the mouth, while the response at high force levels could be important for actions such as biting. Subjects with dentures (who lack the corresponding periodontal ligament receptors), show impaired intraoral sensory perception in tasks as biting force discrimination (Williams et al., 1985). Accordingly, there has been considerable research focus on sensorimotor reflex arcs in which periodontal ligament receptors contribute a signal allowing control of the torques exerted at the temporomandibular joint. There are two key classes of periodontal ligament receptors (Capra, 1995). Those that project to the mesencephalic trigeminal nucleus largely consist of Ruffini-like nerve endings. However, although most Ruffini-like receptors are normally slowly-adapting, these receptors have several specific properties: they are fast adapting, they show directional sensitivity, and their responses covary with the force applied to the tooth. Thus, they are well positioned to code forces on the tooth. Moreover, these have an inhibitory connection to jaw motor neurons in the supratrigeminal nucleus, suggesting a protection against excessive force production in masticatory function (Kidokoro et al., 1968). For example, these afferents could be part of a control loop that prevents damage due to the occasional stone sometimes encountered while eating lentils. In contrast, the apical region and the more superficial structures of the ligament contain both fast and slowly-adapting mechanoreceptors, that connect to the sensory trigeminal nucleus (Trulsson, 2006).

Primary somatosensory ability has often been measured using two-point discrimination tasks. These test the ability to discriminate between two closely-spaced stimuli, and a single stimulus at the central location of the pair. The two-point discrimination threshold is the closest separation at which two stimuli can be discriminated from a single stimulus, and is a useful measure of somatosensory spatial resolution. The two-point discrimination threshold reflects the density of receptor innervation in the stimulated tissue. Thresholds were lower in midline regions compared to lateral aspects of the same oral structure (Ringel and Ewanowski, 1965). Two-point discrimination was impaired when topical anaesthesia is applied to the oral structures, suggesting an involvement of superficial mechanoreceptors in discriminating between two points in the oral cavity (Engelen et al., 2004). Interestingly, subjects were found to display 'sensory sidedness', the phenomenon that discrimination on one of the lateral aspects of the oral structures was superior to the other (Lass et al., 1972).

3.2. Sensations associated with individual afferent fibre types

Microneurography is a technique that allows the contribution of individual afferent fibre types to conscious perception to be studied. Trulsson and Essick (2010) inserted a small microelectrode percutaneously into the lingual or alveolar nerve of awake human participants. By recording the electrical response in the nerve while stimulating different oral tissues, they could discriminate the firing of individual neurons, and identify the stimuli that preferentially activate them. In particular, they were able to identify the spatial receptive field, and the mechanical parameters encoded by each neuron. Crucially, when the neuron was then directly stimulated electrically through the same electrode, but without any peripheral stimulation, participants reported a percept that corresponded in location and quality to the stimulus that best activated the afferent. For example, fast-adapting afferents could be identified by their electrical response to the onset of a mechanical stimulus on the lip, oral or lingual mucosa, coupled with absence of any ongoing response to a sustained

stimulus. Stimulating some of these afferents (type FA I) produced a precisely localised sensation of vibration, with a perceptual frequency that depended on the frequency of electrical stimulation. Slowly-adapting afferents responded to sustained pressure on individual teeth, and were classified as innervating periodontal ligament receptors. Other slowly-adapting afferents responded to specific regions of the tongue. These showed a relatively high spontaneous firing rate, which generally increased only slightly when mechanical stimuli were applied. Direct electrical stimulation of slowly-adapting afferents via the recording electrode did not produce the strong phenomenal experience associated with stimulation of fast-adapting afferents. In some cases (type SA I), localisable sensations of sustained pressure and deep tissue distortion could be obtained, a finding consistent with the response properties of these receptors in monkeys (Price et al., 1976). In other cases there was no detectable sensation at all. It seems likely that stronger stimulation, activating populations of several fibres is required for slowly-adapting afferents to elicit conscious sensations (Trulsson and Essick, 2010).

Trulsson et al. (2010) speculated that the ongoing discharge from slowly-adaptive fibres may contribute to the background maintenance of a persistent “mouth image” – however there appears to be very little direct evidence for this functional role, other than the weak phenomenology associated with both SA afferent input, and with mouth image. Other possible functions of SA afferent systems include regulation of masticatory force, and of oral posture and motor control (Trulsson et al., 2010). The overall picture that emerges from microstimulation studies suggests that light-touch vibrotactile stimuli are among the most powerful perceptual oral experiences. Sensations from deep receptors are less phenomenally vivid, often failing to produce a sensation that matches the receptive field of the afferent fibre (Trulsson and Essick, 2010). This has clear implications for the subjective experience of the mouth through self-touch with the tongue, and the perception of objects in the mouth, such as oral devices, and even foodstuffs.

This conclusion was reinforced by a recent psychophysical study by Hagura et al. (2013). They reported a phenomenally vivid sensation obtained by selectively activating fast adapting mechanoreceptive fibres by a novel chemical means. They used Szechuan pepper to produce an anomalous, substitute activation of fast adapting receptors on the lip, without any mechanical stimulation. Previous studies had identified that the active ingredient in Szechuan pepper (5-hydroxy-sanshool) activates receptor molecules that are preferentially expressed in the membranes of RA mechanoreceptors, notably the 2-pore potassium channel (Bautista et al., 2008). Consistent with this biochemical and physiological specificity, Szechuan pepper was found to produce a touch-like percept of ‘tingle’, with a measurable temporal frequency around 50 Hz. Moreover, mechanically adapting the lip with 50 Hz vibration produced comparable shifts in the perceived frequency of both vibrotactile stimuli and sanshool-induced tingle (Hagura et al., 2013). Thus, even though the peripheral stimulus was chemical and continuous, the percept evoked corresponded to temporally-patterned mechanical stimulation, according to the class of RA fibres that was anomalously activated as a result of the specific receptor chemistry involved.

Other important mechanoreceptors can be found in the temporomandibular joint. Anaesthesia of this joint causes errors in jaw positioning (Broekhuijsen and van Willigen, 1983). These mechanoreceptors are primarily concerned with the proprioceptive sensation of lower jaw position, and may not contribute to sensation internal to the mouth itself.

In summary, the existing literature suggests a vivid oral phenomenology of light, time-varying touch arising from superficial

receptors, and a background phenomenology arising from deeper receptors.

3.2.1. Nociceptors

Pain is a further phenomenally strong signal arising from the mouth. The general function of the nociceptive system is to detect potentially noxious mechanical, thermal or chemical stimuli. Many nociceptive fibres originate in free nerve endings in the tongue, gums and other oral tissues. The tooth pulp also houses nociceptive sensory fibres. In healthy teeth, these show strong discharges only when high forces are applied to the crown, or unusually hot or cold temperatures are experienced on the tooth (Capra, 1995). Nociceptive fibres generally have a smaller diameter and lower conduction velocity than mechanoreceptive fibres. Two types are distinguished based on afferent fibre morphology. A-delta fibres are myelinated and relatively fast-conducting, though still slower than mechanoreceptors. They are responsible for fast, sharp sensations of “pinprick” pain, sometimes also called “first pain”. C-fibres are unmyelinated and slow-conducting, and innervate all parts of the body. They are responsible for dull, slow aching pain, sometimes also called “second pain”.

Although the tooth pulp was previously thought to be innervated only by nociceptors (A-delta and C-fibres), recent research has found that some A-beta fibres also innervate the dental pulp. Kubo et al. (2008) applied innocuous stimuli to the tooth pulp and used magnetoencephalography (MEG) to record magnetic responses in the primary somatosensory cortex resulting from the stimulation of these nerve cells. Peak latencies (the delay between stimulation of the nerve fibre and resulting brain activity) provide information about the type of axon that carries the stimulus, since the speed with which the signals are transported is a property of the type of receptor involved in sensory processes (Kubo et al., 2008). In this experiment, the peak latencies that were recorded in S1 were short – around 27 ms – which suggests an activation of A-beta nerve fibres in the dental pulp. A-beta fibres in other parts of the body are involved in touch, and no conclusive evidence is found on the role of A-beta receptors in nociception in humans (for animals, see Djouhri and Lawson (2004) or Dong et al. (1993)). More research into the function of these fibres is required. For example, they may serve both a mechanoreceptive and nociceptive function. Alternatively, they may be involved in ‘prepain’, a tingling sensation that is reported after stimulation of the tooth crown (Chatrian et al., 1982; Fried et al., 2011; Kubo et al., 2008).

Besides nociceptors in the tooth pulp, the other orofacial tissues are also innervated with nociceptors. Primary nociceptive afferents carry impulses from the oral tissue to the trigeminal spinal nucleus, also called the trigeminal brainstem nuclear complex. This complex extends from the pons to the upper cervical cord. It can be subdivided into subnucleus oralis, subnucleus interpolaris and subnucleus caudalis (Ong and Seymour, 2003). A-delta and C fibres from the oral tissues mostly enter the brain through the subnucleus caudalis, the most caudal of the three nuclei (Price et al., 1976; Sessle, 1987a, b).

From the subnucleus caudalis, three types of neurons project to the thalamus: (1) wide dynamic range (WDR) neurons, responding to both noxious and non-noxious stimuli, (2) nociceptive-specific neurons (NS) and (3) low-threshold mechanoreceptors. The last category does not receive nociceptive input (Amano et al., 1986; Ohya, 1992; Ong and Seymour, 2003). Since a key peripheral input to the subnucleus caudalis comes from nociceptors, this structure is strongly implicated in trigeminal nociceptive processing. Many nociceptive-specific classes of trigeminothalamic neurons are somatotopically organised and have small receptive fields (Price et al., 1976). However, other NS neurons and WDR neurons have larger receptive fields and respond to several modalities of stimuli, such as noxious thermal and noxious mechanical stimulation, or

non-noxious mechanical stimuli (Amano et al., 1986; Sessle, 2000; Yokota, 1989). Price et al. reported 'class 3' trigeminothalamic neurons that responded both to light touch at a latency consistent with A-beta innervation, but also showed a later response consistent with a C polymodal input. Other WDR neurons responded to noxious stimuli from a large range of oral areas including the temporomandibular joint, tooth pulp, masticatory muscles and superficial skin. The coarse spatial tuning of this latter class of neurons suggests that these could play a role in referred pain (Sessle et al., 1986; Takahashi and Yokota, 1983). The large receptive fields and multimodal responses of these caudalis neurons are consistent with the convergent characteristics of neurons and the increase in size of receptive fields when ascending the processing hierarchy (Price et al., 1976; Warren and May, 2013).

3.2.2. Thermoreceptors

The oral tissues are subject to frequent changes in temperature. Thermal sensations in the oral cavity can be of a noxious or non-noxious nature. Trigeminothalamic neurons more frequently responded to warming in the noxious range (above 45 °C) than to warming in the non-noxious range (35–45 °C) (Price et al., 1976). These thermoceptive neurons were judged to receive A-delta or C-fibre input. The number of neurons recruited increased with temperature (Price et al., 1976), with more of these neurons responding at increasing temperatures.

Thermoceptive afferents in the oral cavity are thought to resemble those elsewhere in the body. The afferents that innervate the tooth pulp provide an exception to this rule: they are thought to respond to both noxious mechanical and noxious thermal stimulation, but not to other stimuli (Ahn et al., 2012). Several studies investigating non-noxious thermal thresholds have reported that the oral cavity is less sensitive to warming than facial areas, but equally sensitive to cooling (Essick et al., 2004; Green and Gelhard, 1987; Stevens and Choo, 1998). The tip of the tongue provides an exception to this generalisation. Indeed, within the oral cavity, the thermoreceptors of the tongue are the most sensitive to changes in temperature (Green and Gelhard, 1987).

The normal reason for temperature changes in oral tissue is the presence of a hot or cold object, typically food or beverage, in the mouth. Thus, the primary function of oral thermoception may be exteroceptive – to represent the properties of the object – rather than proprioceptive.

4. Somatosensory cortices and oral sensations

The sensory fibres pass from the periphery within the 3 main divisions of the nerve (ophthalmic, maxillary, and mandibular) to their cell bodies in the trigeminal ganglion situated on the floor of the middle cranial fossa. From the ganglion, the sensory nerve fibres pass centrally to the trigeminal nuclei in the brainstem at the level of the pons, and thence to the thalamus and cortex (Walker, 1990, Fig. 2).

For the purposes of somatosensory awareness, a key destination of all these afferent signals is the somatosensory cortex. Our discussion of cortical bases of somatosensory awareness focuses mostly on the human and non-human primate. The primary somatosensory cortex in humans (SI) forms a strip extending mediolaterally immediately behind the central sulcus. It comprises Brodmann's areas 1, 2, 3a and 3b. The individual Brodmann areas within SI show predominance of particular classes of afferent input, with area 1 and 3b receiving primarily cutaneous afferents, and areas 2 and 3a receiving more deep and proprioceptive inputs. Several somatosensory studies suggest that activation of the primary somatosensory cortex is necessary to achieve conscious sensation (Libet et al., 1979), and direct electrical stimulation of the primary

somatosensory map, for example in humans undergoing neurosurgical interventions is sufficient to produce localised sensory experiences in the corresponding part of the body (Penfield and Rasmussen, 1950).

The secondary somatosensory cortex (SII) lies on the upper surface of the Sylvian fissure, and forms part of the parietal operculum (Eickhoff et al., 2006). Human neuroimaging and primate recording studies suggest that the secondary cortex responds to more complex somatosensory stimuli, such as combinations of tactile and proprioceptive stimuli (Fitzgerald et al., 2006), and to nociceptive stimuli (Lockwood et al., 2013). Moreover, SII neurons have larger receptive fields than SI neurons, which often include homologous skin regions on both sides of the body (Iwamura et al., 1994). Mazzola et al. (2006) electrically stimulated the somatosensory cortex in epileptic patients. They found that merely sensory sensations were evoked by stimulating SI. When stimulating SII, on the other hand, more complex sensations were reported by patients, including pain and non-somatosensory sensations. It is often therefore considered a region of more complex somatosensory integration than the primary somatosensory cortex, where a separate somatotopic map for pain has been reported (Mazzola et al., 2006).

Understanding the organisation of afferents from the mouth to primary somatosensory cortex is therefore important for the basis of oral somatosensory awareness. Several studies in primates confirmed the arrival of oral afferent signals in the somatosensory cortex of primates, and described their receptive fields (see Kaas et al., 2006; Toda and Taoka, 2006 for reviews and summaries). Recent technical advances in neuroimaging has made high-resolution cortical somatosensory mapping possible in humans (Serenio and Huang, 2006). However, the difficulty of providing precise, controlled stimulation of oral tissues in the fMRI environment has limited progress. Most studies have focussed on identifying the mouth area of SI, or particular sub-regions of the oral tissue, relative to representations of other body regions. Surprisingly few studies have combined neuroimaging and psychophysics to consider the role of SI in oral perception and awareness. In addition, the range of different stimulus types, stimulation sites and neuroimaging analyses means that the literature is rather heterogeneous. One recent meta-analysis therefore attempted to combine data from 6 fMRI experiments to investigate the brain projections of oral sensation (Lin et al., 2014). This study focussed only on pain perception provided by pulpal electrical stimulation, so its results may not generalise to other somatosensory modalities. Nevertheless, qualitative and quantitative meta-analysis showed that dental pain activates most of the key brain areas associated with pain in other body sites, notably the thalamus, insula and cingulate cortices. Interestingly, however, the data regarding activation of the somatosensory cortex were mixed: left-hemisphere activation, bilateral activation and absence of activation were all reported by the various different studies that were meta-analysed. Quantitative meta-analysis was also inconclusive. For these reasons, we use this section to review in detail a number of studies which have investigated cortical correlates of oral somatosensory stimulation, paying attention to the different stimulus classes, and the specific activation patterns found.

Several studies have tried to resolve the cortical projections of different structures within the oral somatosensory system. For example, Nakahara et al. (2004) used MEG to map the lips, gingiva and tongue in S1. They found separate cortical areas that represented the lips and the tongue, with no clear separate area for the gingiva. Miyamoto et al. (2006) aimed to extensively map the oral somatosensory region in the left postcentral gyrus, by recording fMRI responses to mechanical stimulation of the lips, tongue and teeth on the right side of the mouth region. The results revealed two gradients within the postcentral gyrus. Most rostrally, in the region classically defined as the primary somatosensory cortex,

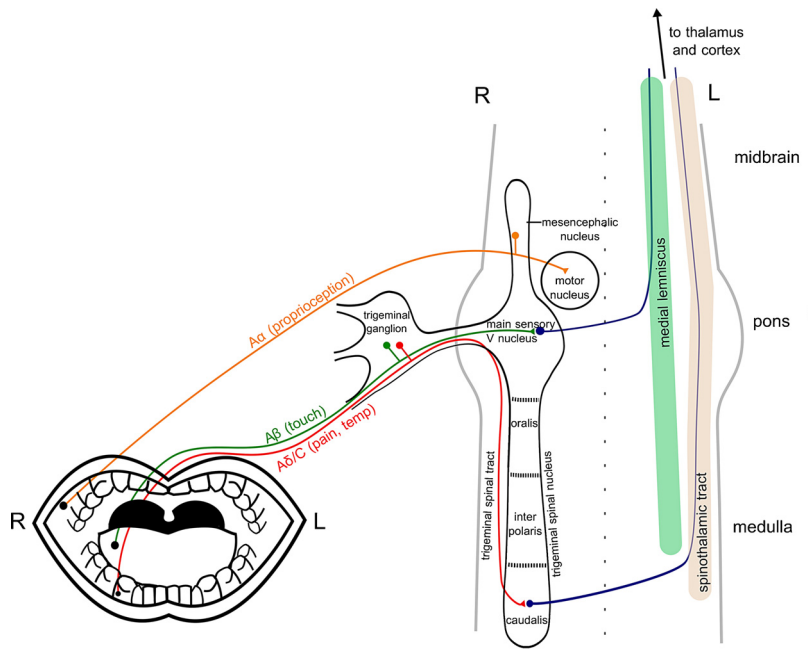


Fig. 2. Schematic overview of the sensory innervation of the oral cavity. Three nerve fibres are used as an example: (1) A discriminative touch nerve fibre (A-beta) on the tongue, (2) a pain/thermoceptive fibre (A-delta/C) in the tooth pulp and (3) a proprioceptive nerve fibre (A-alpha) in the muscles of mastication. Axons from touch and pain fibres in the lower jaw have their cell bodies in the trigeminal ganglion, which they enter through the mandibular division of the trigeminal nerve (V). The touch fibres then synapse with second-order neurons in the principal sensory nucleus in the brain stem. These fibres cross to the opposite side, and ascend to the thalamus via the medial lemniscus. Small-diameter pain and temperature fibres have their cell bodies in the trigeminal ganglion. From there, they descend down to the most caudal division of the trigeminal spinal nucleus (also referred to as nucleus caudalis), where they synapse with second-order neurons. These fibres also cross to the opposite side, and ascend to the thalamus via the spinothalamic tract. Lastly, proprioceptive fibres from the muscles of mastication, and from some periodontal ligament receptors, enter the brain stem via a small branch of the trigeminal nerve. Their cell bodies are in the mesencephalic nucleus. These fibres then synapse in the trigeminal motor nucleus, thereby influencing orofacial motor responses (Linden and Scott, 1989).

they found the superior-inferior gradient established by the sensory homunculus, with the lips located dorsally the teeth, and the teeth dorsally to the tongue. Interestingly, these skin sites were less distinctly localised in more caudal parts of the postcentral gyrus, where overlap of cortical projections was greater.

This gradient suggests that the initial representation of oral somatosensory input is strictly somatotopically organised, but that subsequent processing in more posterior areas may involve integration across different oral tissues. This gradual abstraction from the receptor surface may form a more general representation of the mouth as a whole. Thus, oral somatosensory processing appears to follow a rostro-caudal gradient from primary towards higher processing, as does that for other skin regions such as the hand. This gradient could reflect either peripheral or central mechanisms. First, it may correspond to the different cortical projections of spatially-precise superficial afferents and spatially-broader deep afferents. Alternatively, it could correspond to progressive integration of multiple somatosensory RFs, corresponding to the transition from oral sensation to mouth image. However, a limitation of the Miyamoto et al. study was the form of tooth stimulation, involving manual application of force to the upper incisor with a stick: the forces and direction may not have been precisely controlled, and the findings may not generalise to other teeth (Fig. 3).

Bessho et al. used electrical stimulation to stimulate three regions of the hard palate in humans (Bessho et al., 2007), and recorded the resulting activations with MEG. They found a small palatal region anterior and inferior to the hand area in primary somatosensory cortex (SI), but could not localise independent areas for the three stimulation sites. This suggests that palatal somatotopy is coarse at best. Kubo et al. (2008) stimulated the tooth pulp electrically, and recorded the results with MEG. They were able to identify a specific region within SI responsive for tooth pulp.

Importantly, no such activation was found when the same stimulation was given to teeth lacking pulp afferents as a result of disease (Kubo et al., 2008).

Ettlin et al. (2004) applied vibratory tactile stimulation to maxillary and mandibular teeth during fMRI. Interestingly, they did not find any significant activation of SI, but instead found activation of the supplementary motor area, and of the insula bilaterally.

Jantsch et al. (2005) used fMRI to compare the brain activations caused by painful mechanical stimulation of the teeth and hand. They identified several differences between the activations caused by stimulation at these two sites, over and above those predicted from simple somatotopy. Tooth pain caused bilateral activation of SI, while manual pain caused only contralateral activation. Further, tooth pain caused more extensive activation of the anterior cingulate cortex, which has been widely associated with the arousing and affective aspects of painful stimulation. These results could be interpreted in two ways: they might indicate a specialised and powerful representation of oral structures within the cortex, or they might simply reflect the high sensitivity of teeth as opposed to hands (Jantsch et al., 2005).

Relatively few studies have specifically considered representation of teeth in SI. Shimazaki et al. (2012) use functional near-infrared spectroscopy to evaluate the cerebral blood flow evoked by vibrotactile stimulation of different tooth types. They found a stronger response to stimulation of the first molar than to the other teeth tested (Shimazaki et al., 2012). However, their method had insufficient spatial resolution to identify precisely the size or arrangements of cortical territories for the different teeth.

Habre-Hallage et al. (2012) used fMRI to investigate the neural activation caused by punctate mechanical tapping on an incisor tooth, or on an endosseous oral implant. They also tested 10 control subjects without implants, whose data provide an insight into

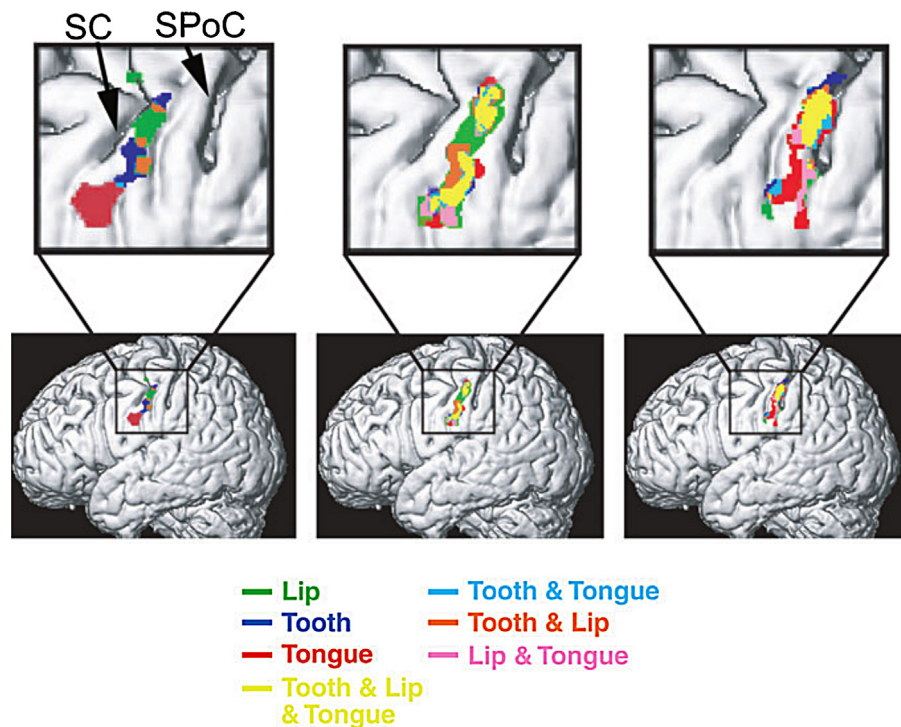


Fig. 3. Representation of different perioral tissues in the human somatosensory cortex. Three maps are shown, extending from the central sulcus (CS) rostrally (left panel) to the postcentral sulcus (SPoC) caudally (right panel). The activations associated with each site of stimulation are more distinct rostrally than caudally. Reproduced with permission from Miyamoto et al. (2006).

the normal cortical activation resulting from stimulating a single tooth. They observed bilateral activations in the primary and secondary somatosensory cortices from such stimulation (Habre-Hallage et al., 2012).

Guest et al. (2007) investigated the fMRI activations associated with introduction of liquids of different innocuous temperatures into the mouth. While the focus of this small study was on the relation between temperature and pleasantness of oral stimuli, some of their results are relevant to other aspects of oral somatosensation. In particular, they found a bilateral activation of the somatosensory cortex during presentation of a hot (50 °C) liquid, compared to a neutral (20 °C) liquid, which survived whole-brain correction for multiple comparisons. Less stringent statistical criteria confirmed SI activation to both hot and cold (5 °C) liquids. Interestingly, this area was not activated by glucose solution at neutral temperature, suggesting that the SI response is purely thermoceptive, rather than hedonic or gustatory. Thus, this study is consistent with a noxious thermoceptive input to the primary somatosensory cortex. In further analyses, the authors suggested that the hedonic aspects of oral temperature are coded in the insula, where they overlap substantially with taste coding (Guest et al., 2007). Although such extreme temperatures can activate nociceptors, the small (1.5 ml) volumes used were not sufficient to produce pain. Therefore, the insula activations in this study presumably reflect thermoception rather than nociception.

Surprisingly, all of these stimuli were reported to be innocuous, even though such extreme temperatures have been reported to produce pain.

In summary, several studies in humans confirm a bilateral projection from oral afferents to the ventral part of the primary somatosensory cortex and to the secondary somatosensory cortex. Gingiva, teeth, palate, and tooth pulp representations have all been identified. However, several outstanding questions remain, and we are far from having a complete knowledge of the oral somatosensory cortex. For example, no study appears to have systematically

mapped the projections from the individual teeth, or from adjacent regions of the soft tissue, to corresponding regions of the cortical surface, as has been done for the fingers (Mancini et al., 2012) and perioral facial skin (Sereno and Huang, 2006). Thus, the detailed structure and resolution of the map of oral tissues within the cortex remains very poorly understood. Many neuroimaging studies have used stimuli that are not selective for particular classes of afferents. For example, it remains unclear whether mechanoreceptive and nociceptive fibres project to different subregions of somatosensory cortex, or rather are intermixed, as is the case for the fingers (Mancini et al., 2012). Few studies have investigated possible relations between somatosensory neural activations and measures of conscious sensation (see Guest et al. (2007) for an exception). Finally, there have been few attempts to integrate information across different studies. One meta-analysis of nociceptive pulp stimulation found low consistency across studies in measures of somatosensory cortical activation (Lin et al., 2014).

Given the high plasticity of somatosensory cortical maps (Buonomano and Merzenich, 1998) and the frequent changes in the oral structures (e.g., following tooth extractions, implants, etc.), studies of oral map plasticity in humans would be valuable. A number of studies have found considerable use-induced plasticity of orofacial motor maps in humans and other primates, for example following tongue protrusion training (see Martin, 2009, for a review). However, oral somatosensory plasticity has been less well studied in humans. On the other hand, invasive studies in rodents have shown that extraction of an incisor is followed by extensive somatosensory cortical reorganisation. Neurons in the somatosensory cortical territory corresponding to the extracted tooth in control animals were found to develop responses to adjacent oral and perioral tissues following extraction (Henry et al., 2005). Another study found changes within one week of incisor extraction in motor responses to intra-cortical micro-stimulation, in somatosensory cortex as well as in motor cortex (Avivi-Arber et al., 2010).

4.1. Comparative studies of somatosensory cortex in primates: anatomy and physiology

Although this review focuses primarily on the human literature, some important comparative information comes from studies of representation of oral structures in the somatosensory cortex of non-human primates. Primate area 3b is thought to be homologous to the primary somatosensory cortex in humans, based on its responsiveness to touch receptors. Around one third of this area is devoted to orofacial structures (Iyengar et al., 2007).

Jain et al. (2001) found distinct oval areas located lateral to hand area within 3b, that were responsive to light taps on the facial structures of New World monkeys. Rostral to the face area, a further group of myelin-rich oval areas were responsive to light taps on structures within the oral cavity. The facial areas were further subdivided along a caudorostral gradient into representations of the upper face (labelled F1), and lower face (upper lip, F2; lower lip and chin, F3). The oral areas could be similarly subdivided into representations of the contralateral teeth (O1), the tongue (O2) and the ipsilateral teeth (O3) and the tongue (O4), although O3 and O4 were sometimes fused. These results suggest a rather precise somatotopy of oral and perioral structures. Representations of the teeth were always found on either side of the most caudal tongue area, with the contralateral teeth represented on the caudal side, and the ipsilateral teeth on the rostral side. Both contralateral and ipsilateral regions of the tongue were represented. The other oral structures could not be mapped as clearly in area 3b as the tongue and teeth. In area O2, some neurons responsive to sensation on the palate were recorded, but areas sensitive to other oral structures were not found (Jain et al., 2001).

These results were later replicated and extended by Iyengar et al. (2007). They first used electrophysiological recording to map the regions of area 3b receiving mechanoreceptor input from oral tissues. They then injected fluorescent tracers into these cortical sites to identify the connected network of brain areas representing oral structures. Their electrophysiological maps broadly replicated Jain et al.'s descriptions of areas O1 and O2 responsive to the teeth and tongue. In addition, a subregion within O2 was identified that was responsive to taps on the palate. They noted that some tissues are represented in both O1 and O2. Further, the oral representation extended medially and laterally beyond area 3b. Histological analysis showed that the densest tracer label was generally within the injected oval. However, larger injections in O1 and O2 revealed connections to more remote areas, notably the putative gustatory cortex in the lateral sulcus (G), and the orbitofrontal cortex (OFC). This research points to an integrated oral sensory network in the brain, including both mechanoreceptive S1, and also chemosensory and hedonic/affective areas (Iyengar et al., 2007).

The above studies have focussed on area 3b of New World monkeys, due to the accessibility of the somatosensory cortex of these species. Cerkevich et al. (2013a) have investigated the representation of the oral area in macaque monkeys. Injections of anatomical tracers into oral representations in area 3b revealed a large number of corticocortical projections. These included connections with other primary somatosensory areas, the secondary somatosensory areas, and ventral parietal areas. In addition, they found connections between different orofacial regions within 3b. These connections from a primary oral area to additional somatosensory areas recalled those reported previously for orofacial representations and representations of other body parts, and appear to constitute a common architecture across all primates (Cerkevich et al., 2013a). In addition, area G, the putative gustatory cortex, was found to connect to the tongue representation in area 3b.

Cerkevich et al. (2013b) investigated the thalamic inputs to macaque area 3b, by injecting neuroanatomical tracers in the tooth,

tongue and face regions of 3b, and identifying label in various thalamic nuclei. Their results showed that oral areas in 3b receive from multiple somatosensory thalamic nuclei, including ventrolateral and ventroposterior nuclei. Importantly, they were able to distinguish between a tactile portion of the ventroposterior medial (VPM) nucleus, and a parvocellular gustatory portion of the same nucleus (VPMpc). They further showed that injections in 3b labelled only the tactile VPM region, and did not label the gustatory portion. From this evidence, they concluded that the thalamocortical projection to the tongue area of 3b is tactile rather than chemosensory in nature. Gustatory inputs from the tongue may instead follow a route from VPMpc to area G (Cerkevich et al., 2013b). This dissociation of tactile and gustatory thalamocortical pathways in the macaque contrasts with the cortical integration of these modalities found in New World monkeys (Iyengar et al., 2007).

Other neurophysiological studies have provided insights into the functional organisation of the oral somatosensory cortex of macaque monkeys. Some neurons in face S1 displayed directional sensitivity to cutaneous brushing stimulation (Lin et al., 1994a). The somatosensory responses of these neurons were often strongly modulated by orofacial movements. This modulation was specific to the movement performed, since there were strong differences in somatosensory responses during tongue-protrusion and during biting. Moreover, the somatosensory modulation depended on the specific direction of tongue protrusion (Lin et al., 1994b).

Following these findings, Toda and Taoka performed several studies assessing the functional organisation of the monkey somatosensory cortex, recording from several sites extending rostrocaudally from area 3b into area 2. Somatotopic organisation was more prominent in area 3b than more caudally. The upper and lower lips each had their own discrete somatotopic representation in area 3b. In contrast, in area 2 a greater proportion of neurons responded to stimuli on either the upper or the lower lip (Toda and Taoka, 2002a). A similar pattern could be seen in tongue representation, where RFs became progressively larger when the recording site was moved caudally from area 3b towards area 2 (Toda and Taoka, 2002b). Neurons with large and composite RFs were more frequent in area 2 than in area 3b and 1. The overall pattern of results is consistent with progressive convergence of somatosensory neurons along a rostrocaudal dimension (Toda and Taoka, 2004). Interestingly, this convergence frequently integrated information from different oral tissues (e.g., gingiva, tongue, lip) in the same spatial region of the oral cavity. They speculated that these tissues might be stimulated simultaneously during, for example, food intake or oral stereognosis (Toda and Taoka, 2001; Toda and Hayashi, 2010). The structuring principle of somatosensory cortical organisation might therefore be the integration of inputs that co-occur during particular orofacial movements.

5. Somatoperception

Somatoperception refers to the perception of objects via the somatosensory system. Several studies have investigated oral stereognosis, or the ability to judge the spatial form of objects in the mouth. Much of this literature aims at standardised sensory testing to evaluate the effects of dental procedures such as implants on oral sensation. Jacobs et al. (1998) reviewed this clinical literature. The majority of tests used focus on shape recognition, and are essentially oral analogues of haptic shape recognition tasks used for manual stereognosis (Lakatos and Marks, 1999; Lederman and Klatzky, 1987). While this literature has proved clinically useful for rehabilitation of oral function, it has proved difficult to identify the neurocognitive basis of oral stereognosis (Jacobs et al., 1998). First, the movements of the tongue and jaw used to explore shapes

within the mouth cannot easily be measured, so that oral haptic strategies are not as well understood as manual haptic strategies (Lederman and Klatzky, 1987). Second, haptic exploration is, by nature, exploratory and uncontrolled. Therefore, the precise object features, and mechanoreceptors used to perceive oral object form remain unclear.

In one of the few neurocognitive studies in this field, Fujii et al. (2011) used fMRI to measure brain activation during manual and oral stereognosis. Compared to rest, both tasks produced a strong activation of somatosensory and motor cortices, as might be expected, as well as of premotor regions associated with action programming and planning. Interestingly, both oral and manual stereognosis activated the supramarginal gyrus. This posterior parietal area has also been associated with tactile object recognition and tactile length perception on other body parts (Bodegård et al., 2001; Spitoni et al., 2010). This finding is consistent with a gradient of processing in the somatosensory system, progressing from somatosensation in primary cortical areas, to somatoperception in more posterior parietal regions. This gradient appears to apply also for shape perception within the mouth. In the visual cortex, neurons in earlier areas respond to receptor-bound properties, such as stimulus orientation, while neurons in later areas respond with increasing degrees of receptor-independence (Hubel and Wiesel, 1968; Serre et al., 2007).

Finally, Fujii et al. (2011) found two differences between the activations for manual and oral stereognosis. Oral stereognosis activated the insula to a greater extent than manual stereognosis. This may reflect the strong affective importance of many objects in the mouth, for example pleasant or unpleasant-tasting foods. This additional, affective representation is apparently activated even for the neutral stimuli used for stereognostic testing. In addition, the lateral occipital cortex was activated more for manual than for oral testing, even though participants had no visual input of the objects they were handling (Fujii et al., 2011). This finding has interesting implications for body representation. Manual objects appear to be represented both somatosensorially and *visually* in the brain, whereas objects touched by the mouth are represented only somatosensorially. This difference in processing can be attributed to the obvious fact that the oral cavity is not normally visible. Oral somatoperception may not benefit from the same multisensory support as other forms. One possibility is that the oral somatosensory system is relatively encapsulated, and does not participate in multisensory processes of object representation. Alternatively, and more plausibly, oral somatoperception may simply involve a *different* set of multisensory interactions. For example, oral somatosensation is known to combine with chemosensory inputs in taste perception (Lim and Green, 2008).

In addition, the link between manual somatosensation and vision plays an important role in body ownership. Visual feedback is thought to be very important for the sense of body ownership (Cardini et al., 2013; Fotopoulou et al., 2011; Hagura et al., 2012), since it provides an experience of our own and other's bodies as physical objects. However, the interior of the mouth is not often viewed, in comparison to, say, the hand (Fig. 4).

In addition to oral shape perception, a few studies have considered oral size perception. In the oral size illusion, a hole presented to the tongue is perceived as larger than one presented to the fingertip. This difference was dismissed as an artefact of the difference in compliance of the soft tissues in each case (Engelen et al., 2002), though it could conceivably also reflect differences in receptor innervation (Taylor-Clarke et al., 2004). Other studies have focussed on perceiving the size of objects in the mouth. In this literature, interest has often focussed on perceiving the size of a food bolus, since this is critically important in regulating swallowing behaviour. Engelen et al. (2002) reported a high level of accuracy in perception of the size of ball-bearings placed in the

mouth, but noted a reduction in performance when a plastic palate was inserted. They suggested that relative movement of the object between tongue and palate was important in oral size perception. Similar studies on the external skin of the face, including the lip, also found accurate performance (Verrillo et al., 2003). Interestingly, studies on the face found no difference in size perception whether the ball was moved across the skin by the participant themselves or by another person. This suggests that size perception is largely a matter of passive cutaneous stimulation, and that the kinaesthetic input generated by the active movement of one body part to ensure stimulation of another adds little somatoperceptual information.

We speculate that somatoperceptual processing inevitably also involves an element of somatopresentation. Using the mouth to perceive size or shape of an object implies a form of knowledge about the structure of one's own mouth. For example, one can judge the size of an object held between the teeth by encoding the angle of the temporomandibular joint, but only if the perceptual system *also* has information about the length of the mandible. Similarly, comparing the size of an object placed on the tongue to an object held in the hand requires a model of the actual physical sizes of the tongue and hand (de Vignemont et al., 2005).

Studies of manual somatosensation suggested that judgements of suprathreshold size and distance are indeed scaled to a model of the actual physical size of the stimulated body part. Crucially, this re-scaling allows an object to retain the same perceived size as it passes from a skin region of high receptor density (e.g., the fingertip or lips) to one of low receptor density (e.g., the arm or forehead). If object size perception simply used the raw somatosensory code found in the SI homunculus, the same object would feel dramatically different when perceived by different skin regions. In fact, body-sized scaling is incomplete, and perceived object size does vary slightly in proportion to receptor density (Taylor-Clarke et al., 2004). However, this variation across body sites is of a much lower order than variations in receptor density might suggest. For example, an object placed on the tip of the tongue produces a quite different afferent signal from the same object placed far from the tip – yet the perceived difference in size is small. This implies that oral inputs, like manual ones, are rescaled according to a “mouth model” or somatopresentation of the mouth structure. In this sense, a mouth model or mouth image is implicitly present in all somatoperception. In the cutaneous somatosensory system, the angular gyrus in the posterior parietal cortex has been identified with this body-based rescaling process (Spitoni et al., 2010).

Finally, the constant self-touch between mouth parts may play an important role in somatoperception. While most experimental studies have focussed on perception of external objects placed in the mouth, our remarks presumably also apply to perception of the teeth or palate by the tongue.

6. Somatopresentation: an internal model of what the mouth is like

Studies of somatosensory awareness classically distinguished between two representations of the body (Paillard, 1999). The body schema refers to a perceptual representation of the current position of body parts in space. It is proprioceptive in origin, and is unconsciously updated as we move the different parts of the body. The body image allows the brain, for example, to avoid hitting one body part against another during movements of more than one limb. The body image refers to a background, ongoing representation of the structure and nature of the body. It is less concerned with what the body is like, as a physical object. Classically, the body image was considered to be visual in nature, and not rapidly updated with the current state of the body – thus it might store knowledge about body structure and canonical body arrangement









Reference	Form	Size		Material
		Thickness (mm)	Length (mm)	
Berry and Mahood [1]		6	12	Acrylic resin
Shelton et al. [30]		?	?	Plastic
Litvak et al. [22]		5	?	Metal alloy
Landt and Fransson [20] Lundqvist [23]		1	≤10	Acrylic resin
Van Aken et al. [35]		1	10–12	Plastic
Garrett et al. [9]		5	–	Raw carrot
Müller et al. [28]		1.5–4	9	Acrylic resin
Jacobs et al. [15]		4	≤10	Acrylic resin

Fig. 4. Oral stereognosis: an overview of stimuli used to test spatial perception of objects in the mouth.

Reproduced with permission from Jacobs et al. (1998).

in a primarily visual form (Schwoebel and Coslett, 2005). For example, the body image might be required to judge relative positions of body parts (Corradi-Dell'Acqua et al., 2008). Several authors have argued for a link between body image and evaluative feelings about the body (Schilder, 1935). The everyday use of the term 'body image' is heavily based on cosmetic, aesthetic aspects and may be close to this evaluative sense. For this reason, the term body model has been preferred in recent literature.

Longo and Haggard (2010) investigated the body model of the hand, by asking people to point towards the location of the fingertips and knuckles of each digit, and computing the internal configuration of their responses (Longo and Haggard, 2010). Similar approaches have been used to study the face and the entire body (Fuentes et al., 2013). In general, strong distortions of all three body parts were found: in each case errors in localising landmarks suggested that the underlying representation was of a less elongated, wider structure than the actual body (Fig. 5).

No similar studies have been attempted for the mouth. As noted by Fujii et al. (2011), vision input from inside the oral cavity is rare and limited. Perhaps for this reason, the mouth image has hardly been studied. Therefore, it remains unclear, for example, how well people can represent the location of the various teeth classes, whether people are aware of the size, number and arrangement of their teeth. This could plausibly be investigated in an oral version of the hand image tasks described above. It seems likely that judgements about oral structure are based not on vision, but rather on haptic self-touch. In particular, exploration of the teeth by the tongue may carry important perceptual information about the teeth and other oral structures.

We stated above that the body image was classically considered to be a stored, long-term representation of visual origin, reflecting structural knowledge of the body. However, several recent experiments have shown that altered somatosensory afferent input profoundly affects the body image. Most people recognise the experience of an inflated, swollen mouth following dental anaesthesia.

Gandevia and Phegan (1999) found that anaesthetising the thumb lead to a rapid increase in the perceived size of the thumb, as measured by drawing (Gandevia and Phegan, 1999). Since no individual peripheral receptor carries information about the size of body parts, this change in how the body "feels to be" must be a secondary consequence of a change in afferent input, rather than simply the brain reading out the new post-anaesthesia level of the afferent signal.

This study makes an important distinction between the size that the thumb *feels to be*, and the stored knowledge about the size that one knows the thumb *actually is*. The former changes, but the latter does not. In this sense, changes in afferent input may be considered to affect the current body model, rather than a stored body image.

Türker et al. (2005) studied perceived size of the front teeth following a set of lignocaine injections at sites adjacent to the front teeth. The injections were demonstrated to suppress perception of tactile and nociceptive stimuli. Participants had to choose one of a number of drawings showing different sizes of front teeth, according to how large their teeth felt, at different times before, during and after anaesthesia. Anaesthesia produced an increase in the perceived size of the teeth. This was less consistent, and less long-lasting than the increase in the perceived size of the lip caused by the same injections. The authors interpreted the stronger lip and weaker tooth effect in terms of the distribution of afferents from the lip and teeth: whereas the lip has a strong RA innervation, the teeth have primarily SA innervation. This result suggests that the representation of the mouth image may depend strongly on RA afferents (Türker et al., 2005) (Fig. 6).

The mechanism whereby removal of afferent input influences felt body part size is not known. Gandevia and colleagues proposed an interpretation based on short-term changes of cortical representations based on lateral inhibition. Removing afferent input from one body part leads to an enlarged cortical territory for other, often adjacent body parts. The enlargement is due to unmasking of afferent projections that are normally suppressed by lateral inhibition in the thalamocortical pathway. Thus, anaesthesia of a peripheral

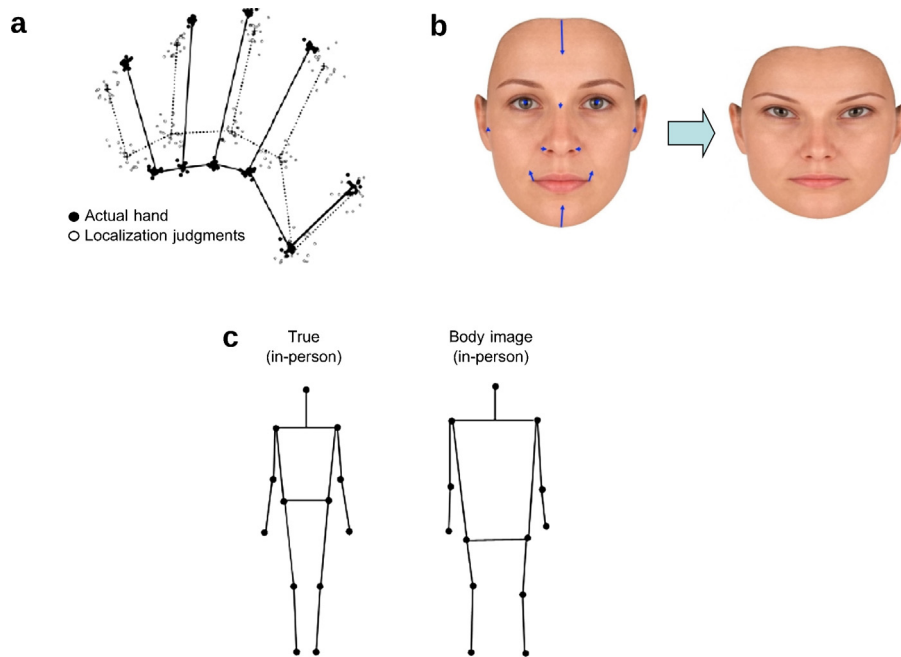


Fig. 5. Perceptual distortions in body representation in the hand (a), face (b) and overall body image (c).

Reproduced with permission from [Longo and Haggard \(2010\)](#) and [Fuentes et al. \(2013\)](#).

region leads to a reduction of the corresponding cortical territory. However, it remains unclear why a *decrease* in cortical representation should lead to an *increase* in perceived size.

7. Somaesthesia: mouth feel

A striking feature of oral somatosensory awareness is the general states of affective feeling within the entire mouth, in the apparent absence of any particular stimulation. Everyone recognises, for example, that the mouth can feel fresh, clean, dirty, dry, “yucky”, and so on. These sensations have a systemic quality: they are poorly localised, and appear to include the entire oral environment. We previously introduced the somatrepresentational level as “what one feels the mouth is like”. However, these evaluative states clearly involve a very different sense of “feel” to the body model. In [Fig. 1](#), we therefore show this evaluative form of oral somatosensory awareness in parallel with the main somatosensory

processing hierarchy. The current section deals with qualitative feeling of the entire oral environment, rather than quantitative perception of spatial properties of individual tissues.

In psychophysical studies, the first step in understanding a ‘feeling’ or sensation is to identify the underlying stimulus that causes the sensation. Somaesthesia is linked both to the physical state of the oral tissue, and to more general homeostatic states. For example, dry mouth feel reflects the level of saliva and other liquids in the mouth. Further, unpleasant feel in the mouth may occur during illness, and can form a strong part of the phenomenology of aversive conditioning: after food poisoning the thought or sight of food is sufficient to induce unpleasant mouth feel ([Frank et al., 1992](#)).

The concept of somaesthesia, is thus highly integrative and multisensory. First, somaesthesia generally involves a combination of several kinds of stimulation: chemical/gustatory input, haptic and tactile input. Second, somaesthesia frequently involves central states of the organism, including the ingestive and appetitive

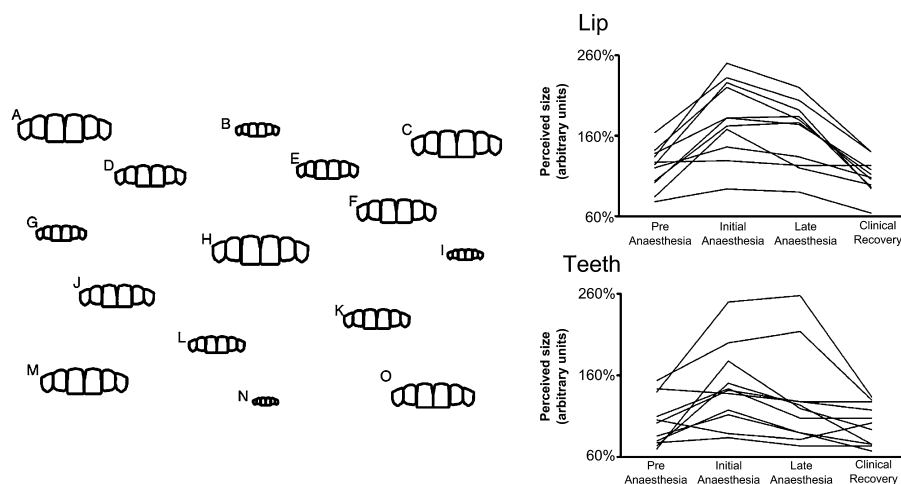


Fig. 6. Effects of local anaesthesia on the perceived size of the teeth, revealed by a template matching task.

Reproduced with permission from [Türker et al. \(2005\)](#).

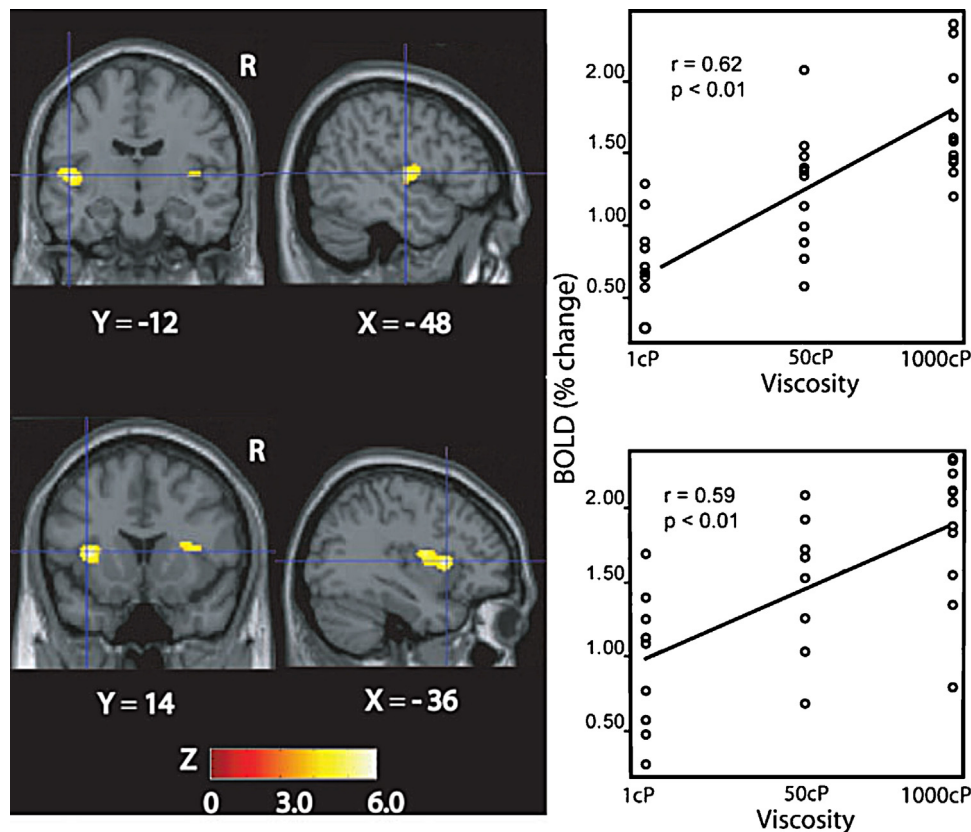


Fig. 7. Brain areas where activation was correlated with viscosity of a liquid placed in the mouth (de Araujo and Rolls, 2004).

systems. Third and finally, the sensory aspects of somesthesia seem inextricably tied to the affective aspects. We noted above the strong coactivation of both primary somatosensory cortex and insula in response to oral stimulation. We suggest this may reflect an early bifurcation between a perceptual pathway leading to oral somatosensation and somatrepresentation, and an affective pathway leading to somesthesia.

The general mouth feel at a particular time is not so much a perceptual representation of individual objects of stimuli, as an emotional-hedonic evaluation of the current oral sensory experience. Perhaps because of this complexity in identifying the stimulus, mouth feel has proved difficult to study quantitatively. However, the literature on perceptions of oral fat is also relevant to somesthesia and the distinction between somatosensory, gustatory and hedonic aspects of mouth feel is not clear-cut. de Araujo and Rolls (2004) investigated the neural processing of oral liquids using fMRI. They compared tasteless cellulose thickening liquids with increasing viscosities, commercial fats and sucrose solutions with a tasteless control. They found several regions of the insula responsive to these oral stimuli. An anterior insula region was responsive to sucrose taste. Delivery of fat activated a more posterior region of the mid-insula, which was not activated by sucrose. This posterior activation to fat could be explained by the viscous properties of the fat, as it was also activated by comparable viscous stimuli. Moreover, the activation in this area was linearly related to viscosity of the non-fatty cellulose stimulus. That is, this region responded to the mechanical rather than chemical properties of substances in the mouth (de Araujo and Rolls, 2004) (Fig. 7).

Interestingly, primary somatosensory areas were not activated above baseline. The authors concluded that the viscosity of liquids in the mouth is coded in a purely somatosensory and taste-independent region of the mid-insula. Importantly, they argued that fats in the mouth might cause two distinct activations within

the insular cortex. The first would reflect the chemical fatty-acid composition of the stimulus, while the second would reflect its mechanical and rheological properties, independent of chemical factors. This double-coding was confirmed in single-neuron recordings from primates presented with fats and non-fatty cellulose stimuli with varying mechanical properties (Verhagen et al., 2004).

The orbitofrontal cortex (OFC) is another area that is activated during the processing of fats. Neurons in this area represent the pleasantness of fat texture (Rolls, 1999; Verhagen et al., 2003), independent of the gustatory effects of fats. Therefore, information that is putatively of mechanoreceptive origin is represented, and linked to the reward value of foods (Rolls, 2012). The mechanical, chemical and hedonic taste aspects of food stimuli appear to be closely integrated. Grabenhorst and Rolls (2013), for example, found activity in the somatosensory cortex when they presented subjects with stimuli of different fat contents and flavours. They found that when subjects were presented with a food stimulus rated as pleasant and high-fat, coupling between the orbitofrontal cortex (OFC) and oral somatosensory cortex was stronger than when presented with a low-fat food of the same flavour. This effect could not be observed between stimuli that were rated as less pleasant in flavour, but that had the same difference in fattiness rating. Thus, activation of the oral somatosensory areas in response to food is enhanced by the fattiness of foods, but only if these foods are also rated as pleasant in flavour (Grabenhorst and Rolls, 2013). The authors therefore propose that the somatosensory cortex is not only active in tactile processing, but also in taste processing (Kaas et al., 2006), and could play a central role in binding together multimodal inputs into a flavour percept (Small, 2008).

These studies have focussed primarily on neural coding relevant to foods. However, foods are a major factor influencing somesthesia, and the general feeling within the mouth depends strongly on food substances and other features of the oral chemical

and mechanical environment. It seems likely that somatosensory/hedonic responses in insular cortex are also involved in mouth feelings in the absence of specific oral stimulation. For example, feelings of cleanness, stickiness, etc. may reflect the presence of films covering the oral tissues. Both the chemical and mechanical properties of these films may be relevant. For example, viscous fluids would profoundly alter the tactile inputs to the tongue as it contacts different oral surfaces. Future research in this area might aim to satisfy a number of requirements. First, it would need to either measure or control the haptic self-touch movements between oral tissues, notably the exploration of the teeth, gums and palate by the tongue. Second, it would need to control and measure the stimulus within the oral environment, and not just at the moment of delivery. For example, the mechanical and rheological properties of liquids will vary with the quantity of saliva present in the oral cavity, and may also interact with saliva production (de Araujo et al., 2003). Third, future research might benefit from assessing psychophysical responses and neural activations corresponding to mouth feel using stimuli designed to target specific afferent fibres. For example, quantitative studies might investigate somaesthesia following administration of menthol, capsaicin, light touch vibrotactile stimulation, and sustained pressure.

8. Conclusion

The mouth has a rich somatosensory innervation, yet there are few systematic studies of oral somatosensory awareness. We have outlined several different levels of oral somatosensory awareness, extending from individual sensations, to integrated perceptions, to a unified 'mouth image'. We have described, based on a theoretical model developed for bodily awareness in general, the specific signals and computations involved at each stage.

There are crucial differences between oral somatosensory awareness and awareness of other parts of the body, and we conclude with a discussion of two such specificities.

First, the multisensory mix for the mouth is unique. Visual input does not play a strong role in experiences linked to the mouth, in contrast to some other body parts, such as the hand. In contrast, self-touch plays a major role in constructing the mouth image, and a much lesser role in awareness of other body regions. Moreover, neuroimaging and electrophysiological studies suggest strong overlap within the brain of the different sensory modalities originating in the mouth. In particular, overlaps between various combinations of mechanical, thermal, chemosensory, and noxious oral stimuli have been identified both in the somatosensory cortex, and in the insula.

Second, oral somatosensory awareness includes an evaluative quality, which we named somaesthesia. Many oral sensations have a strongly valenced quality of pleasantness and unpleasantness, which cuts across the modality of the actual physical stimulus. This somaesthetic aspect of oral somatosensory awareness has a strong link to oral health, and perhaps even to appetite and well-being more generally. However, the signals and circuits that underlie 'mouth feel' remain poorly understood.

Current understanding of higher levels of oral somatosensory awareness is relatively limited. We identified important higher levels of oral somatosensory awareness: perception of objects in the mouth (oral somatoperception), and representation of the nature of the mouth itself (oral somatrepresentation). Both levels seem highly relevant to several applied areas, including appreciation of foods, guidance of oral sensorimotor behaviours such as eating, cleaning and speaking.

Further scientific knowledge of these areas could have important clinical implications, although we have largely focussed on oral somatosensory awareness in healthy humans. The clinical

literature also recognises the importance of sensation for healthy oral functioning (Jacobs and Van Steenberghe, 2006; Sessle, 2006). In particular, somatosensory information from the oral tissues is important in motor control for eating and for speech. Accordingly, a number of clinical tests of oral sensory function have been proposed: stereognosis is one of the most well-established assessment procedures, but other techniques, such as occlusal thickness perception, are also used (Nalbant, 2004). Most studies using these assessments focus on identifying impairments of oral functions in patients with dentures and dental implants (Agrawal et al., 2011; Bhandari et al., 2010). Clinical procedures and interventions, such as extractions, dentures and implants necessarily reduce the somatosensory afferent information reaching the brain, relative to the pre-intervention state (Enkling et al., 2012; Klineberg and Murray, 1999). There has been little quantitative research on the conscious mouth image in clinical conditions, although this seems highly relevant to patient satisfaction with dental interventions.

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