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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 Trulsson 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; Trulsson and Essick, 1997) measure this level of awareness. The second level, which we call *somatoperception*, 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 somatoperception 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