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Review

Force encoding by human periodontal mechanoreceptors during mastication

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ABSTRACT

This overview summarises current knowledge on the force-encoding properties of periodontal mechanoreceptors supplying the human postcanine teeth and describe their signalling during chewing.

Microneurographic experiments reveal that these receptors adapt slowly to maintained tooth loads. Similar to periodontal receptors at anterior teeth, about half respond to forces applied to more than one tooth and their receptive fields are broadly tuned to direction of force application. However, population analyses demonstrate that periodontal receptors supplying anterior and posterior teeth differ in their capacity to signal horizontal and vertical forces, respectively.

Most periodontal receptors exhibit a strongly curved relationship between discharge rate and force amplitude, featuring the highest sensitivity to changes in force at forces below 1 N for anterior teeth and 4 N for posterior teeth. Also the dynamic sensitivity is markedly reduced at high forces. According to a quantitative model of responses in periodontal receptors based on these data, most receptors efficiently encode food contact during chewing, but due to the marked saturation tendencies at higher forces these receptors poorly encode the magnitude of the strong chewing forces and the force changes occurring at these high loads.

Information provided by periodontal receptors is critical for the specification of manipulative forces used when food is positioned between the teeth and prepared for chewing. When the strong chewing forces are applied to crush the food, the receptors signal functionally important information about the mechanical properties of food as well as the spatial contact patterns between the food and the dentition.

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1. Introduction

To control masticatory movements and forces the brain use sensory signals from a variety of sense organs in the orofacial structures. One important source of information is the periodontal mechanoreceptors.^{1–3} These nerve endings are often

described as Ruffini-like and are located close to the collagen fibres in the periodontal ligament.^{4,5} When a force is applied to the tooth, the tooth moves slightly in its socket. This movement induces stresses and strains in the periodontal ligament and the receptors have been shown to respond maximally when the ligament in which they reside is in tension.⁶

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The functional properties of human periodontal mechanoreceptors of anterior teeth and their involvement in the control of biting and food manipulation have been reviewed earlier.^{3,7,8} For that reason, this concise review will focus on the periodontal mechanoreceptors supplying the postcanine teeth primarily used during forceful chewing. Most of the experimental evidence presented is gained from two recent publications by Johnsen and Trulsson.^{9,10} The force-encoding properties of human periodontal mechanoreceptors of posterior teeth will be summarised and their properties will be compared to the anterior receptors. The functional role of these sensors in the control of chewing forces will also be commented on.

2. Periodontal receptors at posterior teeth

By the use of microneurography, signals from single periodontal afferents in the inferior alveolar nerve were recorded in awake human subjects while forces were applied to the surfaces of nylon cubes cemented to the premolars and the first molar on one side.^{9,10} Just like the periodontal afferents innervating the human anterior teeth, these afferents continuously discharge during sustained tooth loads, i.e., they are classified as slowly adapting receptors. Furthermore, most of them are also spontaneously active. The information available from animal studies on the functional properties of receptors at posterior teeth is not totally consistent. Studies on the rabbit and Wistar albino rat report that the majority of periodontal receptors supplying the molars are rapidly adapting.^{11,12} However, in other studies, on the cat and rat, the majority is reported to be slowly adapting.^{13–15}

About half of the human periodontal receptors, irrespective of tooth type, respond to stimulation of more than one tooth.^{9,16} All such receptors show their highest response rate when stimulating one particular tooth, i.e., the receptors-bearing tooth (RBT), with a gradual decline in the response when loading the adjacent teeth. It is clear from the human studies that the RBT is most often an incisor or a canine, indicating a decreasing number of receptors in the periodontal ligaments distally along the dental arch. This finding is supported by several histological studies¹⁷ and attests to the importance of a well-developed mechanoreceptive innervation of the anterior part of the mouth.

3. Directional sensitivity

When loading the RBT in different directions, the periodontal receptors at the premolars and the molars demonstrate diverse and generally wide receptive fields.⁹ Similar to the receptors at the anterior teeth, these receptors typically show excitatory responses in two to four of six stimulation directions tested.¹⁸ In the horizontal plane, the receptor populations at the anterior teeth and the premolars express no clear directional preferences. The receptors at the lower molars, on the other hand, demonstrated a strong directional bias in the distal-lingual direction. In the vertical plane, there is a preference for downward directed forces with a gradually diminishing sensitivity from the anterior teeth to the molars.

The shift from a high sensitivity to most directions at the anterior teeth to the distal-lingual direction at the molars meets the functional demands of the anterior versus posterior teeth. When the anterior teeth are manipulating food morsels and splitting them into pieces in the initial stages of food intake, forces are applied to them in all directions. The molars, on the other hand, grind food substances during more forceful chewing. During the final phase of the chewing cycle, when the lower molars on the working side approach the intercuspal position from a posterior and lateral position, they are likely to experience distal and lingually directed forces upon contact with the opposing upper molar teeth.^{19,20} Given their directional preference for distal-lingual loading, the periodontal receptors supplying the lower molar teeth are well suited to encode information about the forces that normally act on the molars during mastication.

4. Encoding of intensity of chewing forces

A minority of the human periodontal receptors (15–20%), the non-saturating receptors, exhibits a nearly linear relationship between discharge rate and force amplitude and have the capacity to encode force and force changes at quite high forces levels. However, the large majority of the receptors (80–85%), the saturating receptors, exhibits markedly curved stimulus–response relationships, featuring the highest sensitivity to changes in force at forces below ca. 1 N for anterior teeth and ca. 4 N for posterior teeth.^{10,21} Fig. 1 illustrates this by the steeper average stimulus response curve for receptors at anterior (black curve) than at posterior teeth (grey curve). Furthermore, the dynamic sensitivity is both lower and slower for the posterior receptors. The lower static and dynamic sensitivity of periodontal receptors at posterior teeth may just be a result of the different anatomy of posterior versus anterior teeth. Alternatively, it may reflect a functional adaptation of the receptor to the faster and stronger forces that are developed during motor activities involving the posterior teeth.

To describe the responses of human periodontal receptors to arbitrary load profiles a quantitative model was developed that successfully incorporates both the static and dynamic sensitivity of the receptors.²¹ For both anterior and posterior receptors, the modelled discharge rates turned out to be practically identical to those actually measured for novel force stimulations that were not included during the development of the model.^{10,21}

During normal chewing of mixed food the forces exerted on one posterior tooth rarely exceed 50–70 N.²² To predict the discharge from periodontal receptors at posterior teeth evoked during chewing, the subject was instructed to “chew” on a force transducer placed between a pair of molars.¹⁰ The chewing forces that were developed between the molars are shown in the top panel of Fig. 2. Below the force trace is the predicted discharge rates from 10 representative periodontal receptors. Each horizontal row represents the simulated discharge rate profile for one individual receptor: the upper eight are saturating receptors and the lower two are non-saturating receptors.

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