

Afferent sensory mechanisms involved in jaw gape-related muscle activation in unilateral biting

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Abstract

Objectives In unilateral biting or chewing, the working/balancing-side ratio (W/B-ratio) of masseter activities is inversely proportional to the jaw gape which was interpreted as a neuromuscular strategy to protect occlusion. This suggests that jaw separation is afferently perceived, raising the question how this perception might work. In related studies, isometric biting was exerted on rubber pieces that slightly yielded similar to compressed food in chewing. We hypothesized that minor jaw movements associated with this yielding are necessary to elicit a jaw gape-related control of relative activation in isometric biting.

Materials and methods Surface electromyograms of masseter muscles were recorded bilaterally in 20 males during (a) unilateral chewing, (b) isometric biting on rubber pieces inducing jaw gapes of 5, 3, 2, 1, and 0.5 mm, and (c) isometric biting with teeth embedded in rigid splints causing gapes of 5 and 1 mm.

Results With rubber, the masseter W/B-ratio increased from 100 % (5 mm) to 166 % (1 mm) ($p=0.0003$) whereas with the splint it increased just slightly to 112 % ($p=0.005$). With 1 mm gape, W/B-ratios in splint biting were significantly smaller than in rubber biting or in chewing ($p=0.01$).

Conclusions We conclude that minor jaw motion preceding peak force in unilateral biting is necessary to create afferent sensory information that could elicit jaw gape-related activation of masseter muscles.

Clinical relevance Demonstrating a condition under which jaw gape-related activation can lose its occlusion protecting

effect, these findings might contribute to disclose the causes of craniomandibular disorders.

Keywords Jaw gape · Elevator muscles · EMG · Proprioception · Activity ratios

Introduction

When jaw muscles generate a bite force, their relative contributions are supposed to reflect safety or economy principles like minimization of temporomandibular joint (TMJ) loads or muscle efforts [1–6]. Knowledge on this issue commonly refers to static biting with jaw gapes of 5 mm or bigger [2–5, 7, 8]. Muscle recruitment strategies may however change when bite force is applied with smaller jaw separations. This is suggested by the finding that, with decreasing gape in isometric biting or chewing, the masseter working-/balancing-side activity ratio (W/B-ratio) increased [9–11]. This effect was termed “jaw gape-related activation” [10]. It is equivalent to an increasing side-asymmetry of the masseter muscles which is most pronounced at jaw gapes of 1 mm or smaller. In both kinds of motor tasks, the increase of the masseter W/B-ratio was due to a decrease of balancing-side (BS) muscle activity while working-side (WS) activity was about constant. A relative reduction of BS masseter activity in a strong bite or chewing stroke could counteract a vertical approach of BS teeth [11] as induced by tilting of the jaw around the bitten or chewed object [12–16]. It was therefore supposed that the jaw gape-related increase of the masseter W/B-ratio might be a strategy for preventing BS contacts and for limiting loads acting on them in case they occur [9–11]. This strategy implies that neuromuscular control “knows”

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the jaw gape during peak force and adjusts relative muscle activation accordingly. A general ability to perceive a jaw gape is suggested by the fact that humans can discriminate the thickness of interdental objects down to the range of microns [17–24]. Various sensory mechanisms appear suitable for this task, however, little is known about how this proprioception works. Some studies indicated that perceiving a limb's position could be facilitated by prior movements [25–29], especially when these are decelerated [25, 28, 29]. This might also apply to the proprioception of jaw gape in a biting or chewing stroke: In both tasks, peak force is preceded by compression of the rubber or food whereby the jaw moves upward by some tenth of a millimeter and is then decelerated and stopped. It is thus conceivable that these minor jaw movements are important for the proprioception of small gapes. If this would apply, an inhibition of such movements should disturb the afferent feedback which in turn should impede the jaw gape-related activation. While inhibition of these movements is not possible in chewing, it can easily be achieved in biting by replacing the yielding rubber by a rigid splint. The aim of this study therefore was to examine whether inhibition of the minor jaw movements preceding peak force in isometric biting would impede a jaw gape-related relative activation. The null-hypothesis was that the masseter W/B-ratio does not differ between biting on a 1 mm piece of rubber and a 1 mm thick splint.

Materials and methods

Subjects and experimental protocol

Twenty male dental students (mean age, 22.9±3.3 years) volunteered for this study. The subjects had complete Angle Class I or II dentitions and no signs or symptoms of temporomandibular disorders. All subjects gave informed consent to the experimental protocol which had been approved by the Ethics Committee of the Faculty of Medicine at Erlangen University.

Registration of surface EMGs

The electric activities of right and left masseter and anterior temporalis muscles were recorded by means of disposable selfadhesive bipolar Ag/AgCl-surface electrodes with 10 mm diameter of the active area and 20 mm distance between the centers (Type 272 Noraxon, Scottsdale, USA). The electrode locations were determined by palpating the muscle bellies during chewing. After cleaning the skin with alcohol, the bipolar electrodes were attached along the muscle fiber directions. A reference electrode was fixed to the forehead of each subject. The electrodes were clipped to

amplifiers (Biovision, Wehrheim, Germany) with an input impedance of 10 G Ω , a common mode rejection ratio of 120 dB, a noise level of 0.4 μ V, and a bandwidth from 10 to 500 Hz at 3 dB. The amplifiers were connected to a 12-bit A/D-converter (DAQ 6024, National Instruments, Austin, Texas, USA) plugged into a controlling computer (Inspiron 8600, Dell, Austin, Texas, USA). The raw electromyograms (EMGs) of each motor task were sampled for 20 s with a rate of 2 kHz per channel and stored on hard disc. Data acquisition was controlled by in-house software based on the DasyLab[®] programming tool version 8.0 (National Instruments, Austin, Texas, USA). To test correct placement of the electrodes prior to the measurements, each subject performed strong but submaximal intermittent bilateral bites onto pieces of rubber with 1 mm thickness placed on each side. If in this task activities on both sides were strongly different, the electrode with the smaller activity was repositioned. This procedure was repeated until activities on both sides were approximately equal in the bilateral bites.

Experimental tasks

After proper application of the EMG electrodes and setup of the data acquisition system, each person performed the following 16 motor tasks in one session:

Tasks 1 and 2: unilateral chewing of gummi bears. These are gelatine-based-sweets with industrially standardized size and texture (Goldbären, Haribo, Bonn, Germany). One gummi bear was chewed exclusively on the right side, the other one on the left side.

Tasks 3 to 12: unilateral intermittent isometric biting on blocks of silicone rubber with the dimensions of 20×13 mm and heights of 5, 3, 2, 1, and 0.5 mm. Each task was carried out on the right and on the left side separately. The subjects positioned the rubber pieces along the sagittal direction in their area of chewing which encompassed the second premolar and first molar. The rubber pieces were held with the jaw in a non-eccentric position as controlled by the examiner.

Tasks 13 to 16: unilateral intermittent isometric biting on rigid occlusal splints made of bite registration material Futar[®] D (Kettenbach GmbH, Eschenburg, Germany) with thicknesses of 5 and 1 mm on the right and on the left side.

For fabricating the occlusal splints, prior to the measurements, a Futar[®] D strip of about 3 cm length was applied to the lateral mandibular teeth so that it covered the second premolar and first molar of one side. Immediately after application of the registration material, the subject closed his jaw vertically. Closing was stopped by a strip of silicone rubber with either 5 or 1 mm height that was inserted as a distance gauge between the teeth contralateral to the Futar[®] D side. During self-curing of the Futar[®] D

which took about 1 min, the subject held the silicone strip between his teeth without applying a substantial force. After curing, the splints were trimmed to a length of 20 mm. In all isometric tasks, intermittent biting consisted of contraction–relaxation episodes. To ensure isometric contractions, occlusal contact with the rubber pieces or the splints had to be maintained during relaxation. The contractions were performed with a duration and rhythm like in chewing. Likewise, the subjects were advised to generate a peak force like in chewing of gummi bears according to their subjective self-assessment. A jaw gape of 1 mm was considered to be “chewing-like” as this corresponded to minimum interocclusal distances typically reached in consecutive chewing strokes [9–11]. The splint thickness could not be reduced below this limit since the material then became fragile.

Evaluation of data and statistics

The raw EMGs of each muscle obtained in each task in each subject were read into an in-house developed evaluation program based on the DasyLab® programming environment. This software tool rectified the raw EMGs and smoothed them by a gliding average algorithm using 100 points corresponding to an averaging interval of 50 ms. By moving a cursor-delimited window across the time course of the averaged EMGs, the activity peaks achieved during the sequent chewing or biting strokes in each task were determined and entered into an Excel data sheet. From the activity peaks of the four muscles obtained from each chewing or biting cycle, the W/B-ratios of masseter and temporalis muscles were calculated. For each task, the activity peaks and the W/B-ratios were averaged over the number of cycles to obtain task and subject-related mean values. In each subject, the task-related mean values of the activities were normalized to the respective WS values of biting on the 5 mm rubber. Likewise, the mean values of W/B-ratios were normalized to the W/B-ratio of biting on the 5 mm rubber. This normalization was performed for each kind of muscle and was done because jaw gapes of 5 mm or bigger do not influence the W/B-ratios significantly [9]. The normalized task related mean values were averaged over all persons to obtain group mean values of muscle activities and activity ratios for each task. For rubber biting, differences between group mean values at the five different jaw gapes were tested using a one-factorial analysis of variance (ANOVA). If the ANOVA yielded significance, differences between mean values at 5 and 1 mm were tested post hoc by Student's *t*tests for paired data. This *t*test was as well applied ad hoc to pairs of mean values with respect to different gapes (splint biting at 5 and 1 mm), different motor tasks, and different sides. Multiple testing was taken into account by Bonferroni adjustment. A

difference was considered significant if the significance level *p* was equal to or less than 0.05. Statistical results are quoted in the text by the actual Bonferroni-adjusted significance level and the test used. The numeric results are given as mean±95 % confidence intervals.

Results

Muscle activities

M. masseter (Fig. 1)

In chewing, the mean normalized WS masseter activity reached 194±21 %. The BS activity was significantly smaller and amounted to 134±24 % ($p=0.0001$, *t* test).

In biting on the rubber pieces, the WS masseter activity ranged between 100 % and 114±74 % with no significant differences between jaw gapes ($p=0.17$, ANOVA). The BS activity dropped significantly with decreasing gape from 87±12 % with 5 mm to 53±12 % with 0.5 mm ($p=0.0003$, ANOVA). With 1 mm gape, the activity on the BS (64±11 %) was significantly smaller than the corresponding activity on the WS which amounted to 109±12 % ($p=0.0003$, *t*test). In biting on the splint, the WS activity of 128±13 % with 1 mm gape was significantly higher than 110±9 % obtained with 5 mm ($p=0.001$, *t*test). The BS activities however did not differ significantly ($p=0.44$, *t*-test) between 5 and 1 mm gape. The WS activity with the 1 mm splint was significantly higher than the BS activity

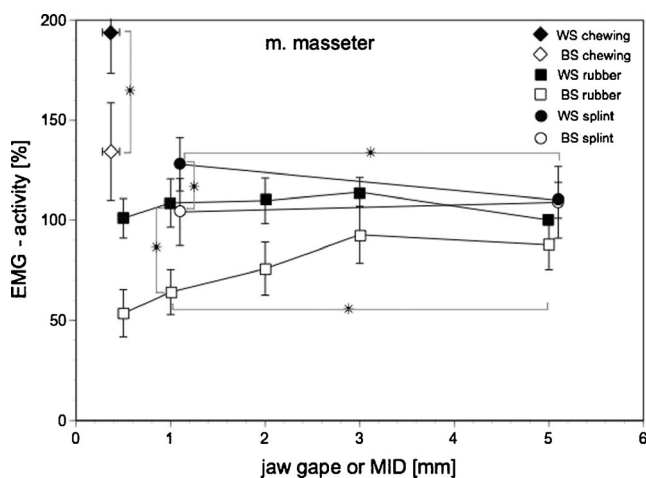


Fig. 1 Group means of masseter activities obtained from the different tasks. The error bars indicate 95 % confidence intervals. Due to normalization, the WS activity in biting on 5 mm rubber appears as 100 % and has no error bar. For clarity reasons, values for splint biting are slightly displaced, and values belonging to the same muscle and task are connected. The stars denote significant differences as described in the text

($p=0.006$, t test) whereas with the 5 mm splint WS and BS activities did not differ ($p=0.9$, t test).

M. temporalis (Fig. 2)

In chewing, the temporalis activity on the WS was significantly higher than on the BS ($p=0.0002$, t test); however, the difference was not as pronounced as with the masseter muscles (Fig. 1). In rubber biting, WS as well as BS activities revealed a significant increase when the gape decreased from 5 to 0.5 mm ($p=0.03$, ANOVA). With all gapes, BS activities were significantly smaller than corresponding WS activities ($P=0.0001$, t test). In biting on the splints, WS and BS activities were both significantly higher with the 1 mm than with the 5 mm gape ($p=0.0002$, t test). With both gapes the activities did not differ significantly from the corresponding activities of biting on rubber ($p=0.2$, t test).

Muscle activity ratios

Masseter W/B-ratios (Fig. 3)

In chewing, the group mean masseter W/B-ratio amounted to 146 ± 18 %. In rubber biting, the ratio increased significantly from 100 % with 5 mm to 189 ± 35 % with 0.5 mm jaw gape ($p=0.0001$, ANOVA). In particular, the ratio with 1 mm (166 ± 27 %) was significantly higher than with 5 mm ($p=0.0003$, t test). The biting ratios with 1 and 0.5 mm gape did not differ significantly from the chewing ratio ($p=0.07$, t test). In biting on the 5 mm splint, the W/B-ratio amounted to 91 ± 8 % and did not differ significantly

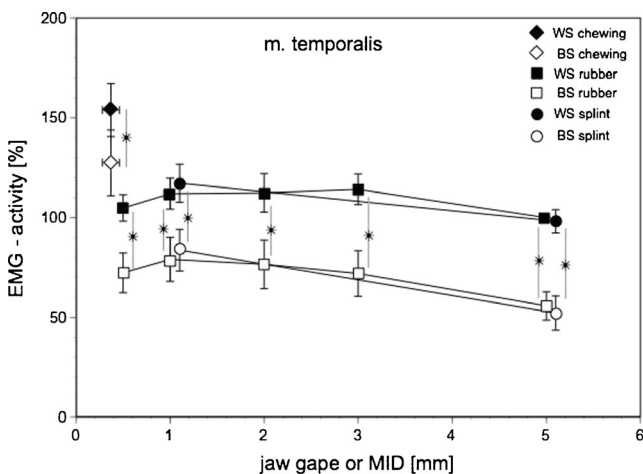


Fig. 2 Group means of anterior temporalis activities obtained from the different tasks. The error bars indicate 95 % confidence intervals. Due to normalization, the WS activity in biting on 5 mm rubber appears as 100 % and has no error bar. For clarity reasons, values for splint biting are slightly displaced, and values belonging to the same muscle and task are connected. The stars denote significant differences as described in the text

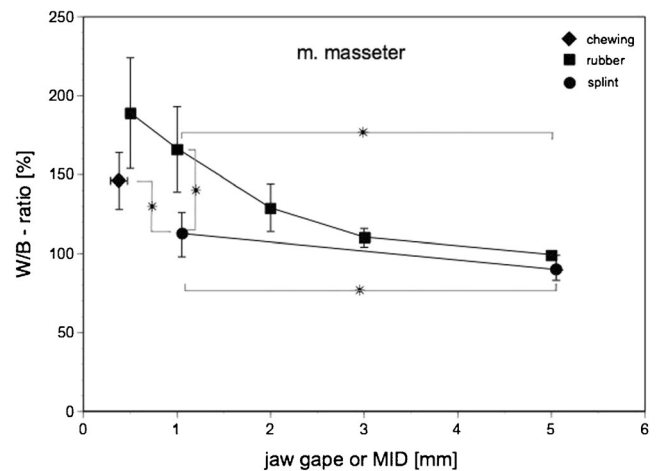


Fig. 3 Group means of W/B-ratios of masseter activities obtained from the different tasks. The error bars indicate 95 % confidence intervals. Due to normalization, the W/B-ratio in biting on 5 mm rubber appears as 100 % and has no error bar. For clarity reasons, values for splint biting are slightly displaced, and values belonging to the same task are connected. The stars denote significant differences as described in the text

from the ratio of biting on the 5 mm rubber ($p=0.08$, t test). In biting on 1 mm splint, the ratio increased significantly to 112 ± 14 % ($p=0.005$, t test) but was still significantly smaller than the ratios of biting on 1 mm rubber (166 ± 27 %) ($p=0.0003$, t test) or of chewing ($p=0.01$, t test).

Temporalis W/B-ratios (Fig. 4)

In chewing, the group mean temporalis W/B-ratio amounted to 75 ± 14 %. In rubber biting, the W/B-ratio ranged between 100 % and 90 ± 16 % but showed no significant differences

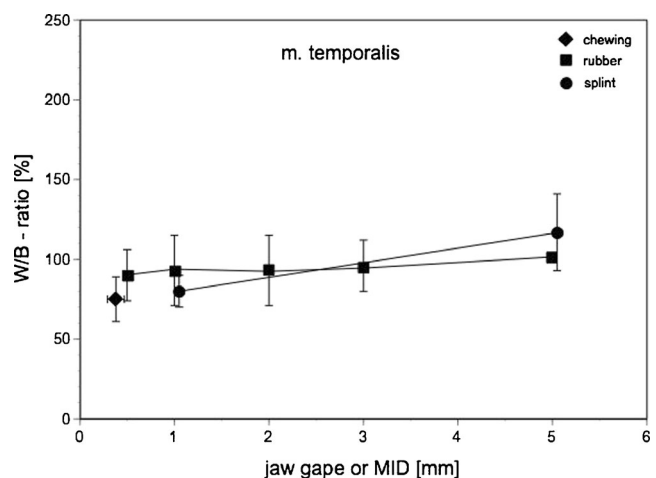


Fig. 4 Group means of W/B-ratios of the anterior temporalis activities obtained from the different tasks. The error bars indicate 95 % confidence intervals. Due to normalization, the W/B-ratio in biting on 5 mm rubber appears as 100 % and has no error bar. For clarity reasons, values for splint biting are slightly displaced, and values belonging to the same task are connected

between the jaw gapes ($p=0.94$, ANOVA). In biting on the splints, the ratio decreased significantly from $117\pm 24\%$ with 5 mm to $80\pm 10\%$ with 1 mm splint thickness ($p=0.0006$, t test). The ratios in biting on the splints did not differ significantly ($p=0.1$, t test) from the ratios in biting on rubber with like jaw gapes.

Discussion

The aim of this study was to examine whether minor jaw movements preceding peak force are essential to induce jaw gape-related relative activation of masticatory muscles when isometric biting is done with jaw gapes as small as in chewing. As for the masseter muscle, this assumption is supported by the results: When rubber thickness in biting was reduced from 5 to 1 mm, the masseter W/B-ratio, in agreement with previous reports [9, 11], increased strongly and approached the ratio of chewing. However, when the same biting procedure was performed with the jaw locked by a splint, the masseter W/B-ratio increased just slightly. In biting on a splint with the chewing-like gape of 1 mm, the ratio was significantly smaller than with rubber of the same thickness and was also significantly smaller than the ratio of chewing. Hence, the null-hypothesis which postulated no difference in W/B-ratios between biting on a 1 mm piece of rubber and a 1 mm thick splint could be rejected. With yielding rubber, a jaw gape-related relative activation was elicited while with the rigid splint it was widely suppressed.

In line with previous results [9, 10], temporalis activities in rubber biting decreased just moderately when jaw gape was reduced (Fig. 4). As neither this decrease of activities nor their differences to the activities of splint biting were significant, the temporalis activation provides no relevant information with respect to the study hypothesis.

An increase of the masseter W/B-ratio with decreasing jaw gape (Fig. 3) has been interpreted as a strategy to prevent overloading of BS teeth or TMJ [9, 10]. Thereby, motor control should sense the jaw gape and reduce the relative strength of the BS muscle accordingly. The latter actually happened in biting on the rubber pieces where BS activity was reduced significantly with decreasing gape while WS activity did not change (Fig. 1). In splint biting, however, the BS activity did not change in response to the decreasing gape, but instead WS activity slightly increased (Fig. 1). Hence, one could argue that, with yielding rubber, the jaw gape was perceived while, with the rigid support, it was not.

To address the question which sensory mechanisms are involved in the perception of a jaw gape, it is reasonable to consider the discrimination of thickness of interdental objects since thereby a jaw separation is induced as well

[17–24]. Thickness discrimination was assumed to be achieved mainly by muscle spindles and/or periodontal receptors [18, 19, 21–23, 30]. This corresponds to current opinions stating that the position of a limb—and hence of the jaw—is sensed by muscle spindles [25, 27, 31, 32]. The latter are firing not only during passive stretch but also during contraction [33] and in particular during the masticatory power stroke [31, 34, 35]. It was even demonstrated that spindle output in rabbits differed between WS and BS muscles [35]. In contracting muscles, spindle output results from γ -activation which stretches the muscle spindles against the shortening of α -innervated muscle fibers. So while muscle spindle discharge per se is evident in contracting muscles, it is not established whether and how this discharge provides a suitable gape-related afferent signal [36–38]. Muscle spindles are divided into secondary endings indicating a muscle's length [27, 32, 39] and primary endings reacting to length changes and hence to movement [27–29, 39, 40]. The fact that BS activity (Fig. 1) and W/B-ratio (Fig. 3) hardly responded to a reduced gape when jaw motion was impeded might mean that stimulation of primary spindle endings by movement may be one prerequisite to elicit a jaw gape-related afferent signal.

A possible influence of movement on position sense was suggested by reports that limb motion can enhance the acuity of kinesthetic perception [26–28] or that slowing down of limb motion could evoke a sense of changed position [27–29, 40]. Comparable findings indicating an influence of jaw movement on jaw gape perception are not directly manifest. However, an influence of jaw motion on thickness discrimination may be inferred from slight tooth tapping movements performed in some experiments [18, 24]. Since tapping was done with light forces [18, 19], fastly saturating periodontal receptors might also have become involved [41, 42]. However, the latter is unlikely to apply to perception of jaw gape in biting or chewing since bite forces were quite high in these tasks.

While periodontal receptors thus seem hardly relevant for perception of jaw gape, other sensory sources [43–45] apart from muscle spindles might contribute. In a unilateral chewing or biting contraction for example, skin tension may change or intraoral mucosa may be touched by the teeth. The sensory output stimulated by such tactile events may depend on jaw gape and minor jaw movement [46] and may combine with spindle discharge to an afferent signal flow [27]. In biting on rubber or splint, this signal flow may be compared in a complex neurological process to an engrained sensory pattern of mastication [27, 32, 47, 48]. Accordingly, a chewing-like masseter W/B-ratio may then be induced (rubber) or not (splint). Finally, a possible role of TMJ receptors for the sensing of jaw gape should not be disregarded. Modelling of human mastication

with an asymmetric masseter W/B-ratio resulted in unloading of the BS TMJ [49]. In contrast, experimental animal studies demonstrated a higher loading of the BS TMJ in the presence of an asymmetric masseter W/B-ratio [50]. Whether the jaw gape-related increase of the masseter W/B-ratio could also be a mechanism for protecting the TMJs thus remains unclear.

Methodological considerations

Our interpretations are based on a surface EMG protocol which corresponded to relevant recommendations for proper experimental practice [51–53]. Despite its widespread use, this method since recently seems to have become the focus of a methodological criticism which is difficult to follow. The main arguments put forth by critics are that EMG signals picked up by one pair of electrodes might be distorted by cross-talk from other elevator or facial muscles, by “grimacing” or by movement of electrodes against the muscle bulk. Like other authors [54, 55], we could not find reliable data about cross-talk between elevator muscles. An estimate of cross-talk would require that routinely contracting muscles can also act antagonistically [56–58]. This is not the case with jaw elevators, since even under cortical control, it was not possible to activate one muscle alone [59]. Assessment of cross-talk between elevator muscles can therefore only be based on observational evidence: In our practical experience, measured EMG signals drop considerably when an electrode is displaced by just some millimeters from the muscle belly. As jaw elevators are however separated by much bigger distances of several centimeters, it is likely that cross-talk is strongly attenuated. In fact, with similar distances, only 5 to 7 % cross-talk was found between leg muscles [58]. It is thus reasonable to assume that activity collected by an electrode mainly represents output of the subjacent muscle overlaid by minor fractions of activities from other muscles. In bilateral pairs of muscles like the masseters, mutual cross-talk activity will emerge in an inverse ratio of the originating activities. If for example WS masseter activity is twice as high as the BS activity, then twice as much cross-talk is induced on the BS than on the WS. Cross-talk thus tends to equalize the surface EMGs which in turn has a dampening effect on activity ratios. Significant differences between ratios as found in the present study were thus not caused by cross-talk but occurred despite it. Unlike with elevator muscles, there are rare but obvious statements concerning cross-talk from facial muscles: Two studies demonstrated that in chewing perioral muscles were activated alternately to the jaw closers [60, 61]. Thereby, a high activity of facial muscles during inactivity of the masseters did not induce observable cross-talk activity in masseter electrodes [61]. Moreover,

the mode of unilateral biting practiced in our study did not favor the emergence of mimic muscle activity since no food was manipulated, lips and cheeks were not moved, and subjects did not laugh or talk. Likewise, grimacing as possibly provoked in case of muscle pain [55] was not observed. Shifts of the muscle bulk against the electrodes during the contraction have been suspected as a further source of artifact [62, 63]. While such concerns may apply to wide limb movements like bending or stretching a leg [64], the two kinds of isometric biting tasks in our study differed by movements of just fractions of millimeters. There is no evidence that this has any influence on EMG. The crucial effect of the present study was that the activity of the BS masseter differed strongly between biting on rubber and on splint. We have no idea how this could be explained consistently by any of the discussed hypothetical sources of artifact. Unless shown otherwise, we join the general belief that surface EMGs represent at least qualitatively the contraction strength of the underlying muscle [54, 56, 65].

In summary, this study demonstrated that minor yielding of a unilaterally bitten object is necessary to elicit a jaw gape-related activation of masseter muscles. If the gape would be sensed by muscle spindles, then these would need a dynamical stimulus to provide the afferent gape-related signal to motor control. The results could however not identify the muscle spindles as the only sensory sources. In follow-up studies, one might try to demonstrate the possible role of mucosal, cutaneous, and periodontal receptors by testing how jaw gape-related activation (i.e., the masseter W/B-ratio) responds to anesthetic deactivation of such sensors. In any case, the relation between jaw separation and relative muscle activation appears to be a promising non-invasive tool for studying motor control strategies and proprioceptive mechanisms in humans.

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Conflict of interest The authors declare that they have no conflict of interest.

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