Long-term training effects on masticatory muscles

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SUMMARY Neuromuscular adaptations during skill acquisition have been extensively investigated for skeletal muscles. Motor rehabilitation is the main target for application of motor training. Such measures are also relevant for the musculature of the jaw, but few data are available for motor adaptation of the masticatory system. The objective of this study was to evaluate and compare long-term training effects of different motor tasks on masseter and temporal muscles. In 20 healthy subjects, the electromyographic response to unilateral and bilateral maximum voluntary tooth clenching, balancing the mandible on a hydrostatic system under forcefeedback-controlled conditions, and unilateral chewing was investigated in an initial session and then in two follow-up sessions separated by 2 and 10 weeks from baseline. Motor tasks were repeated three times for chewing, nine times for maximum biting (MB) and 24 times for the coordination tasks (CT). The sequences of the various motor tasks were applied once in the first session and twice in the second and third sessions. No effects of training were observed for MB tasks except for MB in intercuspation, for which significant yet transient avoidance behaviour occurred in the second session. No significant effects were found for chewing tests. For the CT, however, a robust significant long-term training effect was detected which reduced the electric muscle activity in session 2 by approximately 20% and in session 3 by approximately 40% compared with the initial measurements. The study showed that the masticatory muscles are remarkably prone to motor adaptation if demanding CT must be accomplished.

KEYWORDS: coordination motor tasks, motor learning, temporomandibular disorders, electromyography, motor plasticity

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Introduction

Motor adaptation is the modification of motor actions from trial to trial on the basis of error feedback in which several criteria are met. The motor action retains its identity of being a specific action but changes in terms of one or more variables (e.g. the pattern of force direction). The change occurs with repetition or practice of the behaviour. Once adapted, individuals cannot retrieve the previous behaviour; instead, 'aftereffects' are observed, and the individuals must 'de-adapt' the behaviour with practice (1). Thus, a finite number of 'learned motor patterns' can be adapted to account for many different situations. Adaptation occurs for all types of motor action, for example reaching, walking and balancing (2). Motor learning, in contrast, is used to mean the formation of a new motor pattern that occurs as a result of longterm practice (i.e. days, weeks, years). After the new movement pattern is learnt, it is stored and can immediately be recalled and used in the appropriate context (i.e. in contrast to adaptation, no practice period is required) (2).

Neuromuscular adaptation during skill acquisition has been extensively investigated for skeletal musculature (3–5). It is well known that when first performing novel tasks, the muscle activation used to achieve the objective of the action does not typically use the

muscles available in the most effective manner (6, 7). Because motor tasks are achieved by activating body and limb muscles, changes in performance must be associated with modifications in the pattern of muscle activation (8). Motor training results in performance improvements that are associated with cortical reorganisation (9, 10) and adaptation of the behaviour of motor units (11). The gain achieved as a result of training sessions, however, differs among body components and the applied motor tasks (3, 12). Beside sporting activities, motor rehabilitation is the main target for the application of skill acquisition to promote neuromuscular plasticity at the cortical and subcortical level in patients compromised by cerebral lesions after stroke (13) or painful neuromuscular disorders (14). These questions are relevant not only for the body and limb musculature, however, but also for painful masticatory muscles in patients with temporomandibular disorder (TMD).

In this context, it must be emphasised that regional muscle lesions are assumed to be the basis for acute or persistent (not chronic!) muscle pain (15–18). This may imply that unloading of such compromised motor units might reduce muscle pain (19). Jaw muscles are characterised by small motor unit territories with remarkable directional specificity of force generation (20), which can be differently activated depending on the specific motor task (21–23). These characteristics, in turn, imply that minor modifications of a motor task can recruit different motor units and, in the best case, switch off or reduce the recruitment of painful motor units. Under this working hypothesis, it would be of interest to have motor exercises available that are able to modify the recruitment behaviour of the masticatory muscles in a long-term run.

So far, few studies have investigated motor adaptation of the masticatory system with objectives comparable with those mentioned earlier (24–26). The results demonstrated plastic changes for tongue-task training and for isometric contraction behaviour of the masticatory muscles. It has also been shown that pain hinders, but does not prevent motor learning (25). No data are available, however, for long-term skill retention from demanding novel coordination tasks (CT) simulating comparable balancing efforts, for example, during chewing or isometric contractions with varying interocclusal distances. The objective of this study was, therefore, to test, in healthy subjects, whether balancing tasks, performed in three sessions separated by 2 and 10 weeks from baseline, have a significant effect on motor behaviour. We also tested whether performance of the CT after the training sessions differed from that of established tasks, for example, MB and natural chewing, which were also performed repeatedly in the same sessions.

Methods

Subjects

Twenty healthy students, 10 women and 10 men (average age: 24 ± 2 years), were enrolled in the experiments. Exclusion criteria were painful TMDs or need for orthopaedic treatment. None of the subjects had previously participated in similar experiments. The participants were instructed to refrain from drugs such as alcohol or muscle relaxants, which could affect motor performance during the experiments. The study was approved by the Ethics Committee of the University Medical Centre, Heidelberg (no. S-213/2008). All subjects gave their written consent to the experiments, which were conducted in accordance with the Declaration of Helsinki.

Intra-oral force measurement

Force-controlled biting tasks were analysed by means of a recently developed hydrostatic system (Fig. 1) consisting of liquid-filled plastic pads (components of a commercially available intra-oral hydrostatic device*), which were placed unilaterally or bilaterally between the rows of teeth in the premolar to molar regions (Fig. 2). Before the experiments, the pressure-force relationship was calibrated (Universal testing machine⁺). Bite forces on the pads result in increased hydrostatic pressure within the liquid. This pressure increase corresponds directly to the amount of total force exerted on the pads. Because bilaterally positioned pads were connected, various bite force levels led to different vertical height reductions in both pads, because of increasing deformation. Furthermore, force variations between the left and right sides led to additional vertical height differences between the pads (Fig. 3).

Bite force tasks with different forces performed on unilaterally or bilaterally placed pads provoke the

^{*}Aqualizer[®]; Bausch KG, Köln, Germany.

[†]Zwick/Roell Z005; Zwick GmbH & Co KG, Ulm, Germany.



Fig. 1. Schematic representation of the hydrostatic pressuremeasuring device mounted on intraoral plastic splints.



Fig. 2. Intraoral device of the measurement system: pressuresensitive pads mounted on a plastic splint for bilateral biting experiments.

neuromuscular system to balance the mandible in a manner which may, approximately, be compared with the demands of chewing or clenching in an unfamiliar jaw relationship (e.g. if an orthopaedic appliance is being used). A single chewing cycle may be approximated by a sequence of consecutively changing, quasistatic equilibrium states of the mandible (in particular, during breaking of brittle food with consecutively changing resultant bite force vectors at the food bolus site separated by short unloading episodes) with short initial kinetic phases. The hydrostatic system enabled comparable bilateral or unilateral isometric contractions with initial reduction in the interocclusal separation (kinetic phase, caused by deformation of the pads) and variable vertical occlusal distances (equilibrium states) depending on the bite force applied.

Pressure measurement was accomplished by the use of specific sensors integrated within the hydrostatic system,

which also actuated a feedback monitor with a numerical display[‡] 100 cm away, at eye level. The sensitivity of the display as viewed by the subject was 0.5 N. The pads of the hydrostatic system were paraocclusally fixed by metal pins to a maxillary plastic splint with a plane occlusal surface. Correspondingly, the mandible was also covered by a plane splint (Fig. 3). Depending on the bite force applied, jaw separation ranged from 4 to 6 mm in the molar region. The pressure values were simultaneously documented, at a sampling rate of 1000 Hz, with the electromyographic (EMG) data[§].

EMG measurements

Bipolar surface electrodes measured, bilaterally, the EMG of the masseter and anterior temporalis. Ag/AgCl electrodes (diameter: 14 mm; centre to centre distance: 20 mm[¶]) were placed parallel to the longitudinal axis of the muscles. Before application, the skin was cleaned with 70% ethanol. The common electrode was positioned on the neck above the 7th vertebra. To enable exact repositioning of the electrodes in the follow-up sessions, a special device was developed (Fig. 4); this consisted of a modified arbitrary face bow connected to an individually prepared bite fork. Vertically positioned adjustable flags with pins mounted on the face bow enabled exact repositioning of the electrodes, which were attached to the pins and in this way guided on to the skin surface. The EMG signals were differentially amplified**; (frequency response: 1-5000 Hz) and sampled at 1000 Hz simultaneously with the force signals.

Experimental procedure

The subjects accomplished three differently controlled motor tasks [i.e. maximum biting (MB), unilateral chewing and force-controlled CT at submaximum bite force], which were performed in a predetermined sequence in upright stance. Maximum bites are characterised by control mechanisms which, presumably, are not essentially affected by the redundancy of possible coactivation strategies, i.e. all the muscles involved are

- [¶]Noraxon Dual Electrodes; Noraxon, Scottsdale, AZ, USA.
- **EM 100 Biopac, Santa Barbara, CA, USA.

[‡]PAXS000B-TRG-Z0032; Althen GmbH, Kelkheim, Germany.

[§]AcqKnowledge 3.5 Software; Biopac Systems Inc., Santa Barbara, CA, USA.



Asymmetric equilibrium





Fig. 4. Modified face-bow used for precise relocation of the surface electrodes. Pins and adjustable flags enabled reproducible guidance of the electrodes on to the skin.

activated at their maximum psychophysiological capacity. Chewing cycles involve well-trained muscle action, which essentially represents automatic motor behaviour. Unfamiliar CT, in contrast, provoke the motor control to establish the best-fitting coactivation of the involved muscle groups and have to be adapted sequentially, as is known for novel motor tasks. Upright stance was chosen because this body position integrates the entire postural muscle chain, and we assumed this might

Fig. 3. Effects of the hydrostatic pressure system on the balancing behaviour of the mandible. Symmetric and asymmetric force distribution between the left and right sides of the jaw at static equilibrium are depicted. F_1 , F_2 = bite forces exerted on the plastic pads; h_1 , h_2 = interocclusal distances. P_i = pressure of the system caused by filling of the pads plus the pressure generated by the sum of all external loads (F_1 + F_2).

be an essential physiological basis for experimental motor tasks of the masticatory muscles.

Maximum voluntary jaw clenching tasks (MB) were executed in intercuspation (IC), on cotton rolls placed bilaterally (BCR) or unilaterally (right side UCR) between the posterior teeth. Force-controlled CT were performed unilaterally (right side) and bilaterally at bite forces of 50, 100, 200 and 300 N (subsequently denoted u50 to u300 for unilateral biting and b50 to b300 for bilateral biting). The subjects were instructed to position the mandible in centric relation before biting on the pressure pads. Because the pads were fixed on the maxilla and because of the plane surfaces of the splints, the position of the mandible was automatically stabilised in the posterior position by horizontal force components of the bite force. In addition to mechanical considerations, this issue was confirmed by measurements with an ultrasonic kinematic recording system⁺⁺ (27), which was used in several experiments.

When the test person's biting on the pads reached the intended force, measurements were started. The bite experiments took 5 s each. The intention to avoid muscle fatigue and to make the different static tasks comparable justified the relatively short exposure times. Right side chewing with 15 chewing cycles per chewing sequence was performed with standardised silicone cubes (28). A single bolus consisted of 17 cubes with 5.6-mm edge

⁺⁺Zebris WinJaw, Isny, Germany.

Table 1. Follow-up of the trainingsessions

Sessions	T1	2 weeks	T2	1 h	T2'	8 weeks	T3	1 h	T3′
Replicate MB	9		9		9		9		9
Replicate CT	24		24		24		24		24
Replicate rCH	3		-		3		3		3

MB, maximum biting in intercuspation (IC), unilaterally on cotton rolls (uBCR) and bilaterally on cotton rolls (bBCR); CT, coordination tasks with submaximum biting at 50, 100, 200 and 300 N bilaterally (b50 to b300) and unilaterally (u50–u300); T1, T2 and T3, first, second and third sessions; T2/T2' and T3/T3', sequences 1 and 2 in the second and third sessions, respectively; rCH, right side chewing.

length. The experiments were repeated after 2 and 10 weeks. MB and CT were repeated three times at baseline (T1) and six times, separated into two sequences, at the two follow-up sessions (T2/T2'; T3/T3'). Chewing was repeated three times during sessions 1 and 2 and six times during session 3, separated into two sequences. The total was therefore three replicates for chewing, nine for MB and 24 for the CT at baseline, in contrast to three replicates for chewing, eighteen for MB and 48 for CT in the second session, and six replicates for chewing, eighteen for MB and 48 for CT in the second session, and six replicates for chewing, eighteen for MB and 48 for CT in the third session (Table 1). As a measure of the motor adaptation of the masticatory muscles, we chose changes of the EMG activity of the left and right temporal and masseter muscles compared with baseline (T1).

Data analysis

The raw EMG data obtained from the four muscles monitored were rectified with the root mean square algorithm. By the use of specially developed software, the time at which the test person completed a particular 5 s static bite task (CT, MB) was determined by a preset threshold, and an interval of 4 s was counted back from this point for analysis of the EMG. The rectified data from the fifteen chewing cycles, which lasted between 12 and 15 s, were evaluated from the integral of the EMG recordings (area under the rectified EMG curve). The results from the three replicates of the different motor tasks were expressed as mean values (mean) and standard deviations (s.d.). Intra-individual scatter of bite force and EMG data for the task replicates were clarified using coefficients of variation (cv). EMG differences for the muscles during chewing tasks among the sessions were compared using one-way repeated measures (RM) analysis of variance (ANOVA). Different muscle activities in the experimental sessions for MB, unilateral and bilateral feedback-controlled CT and sex differences were investigated by two-way RM ANOVA. The significance level was set to P < 0.05 for all analyses. Post hoc Tukey tests were used for further analysis of differences. The Software SPSS 17.0 for Windows^{‡‡} was used for the statistical analyses.

Results

Intra-individual variability (cv) for the three measurement replicates averaged over all motor tasks was $15.8 \pm 2.5\%$. The relative difference of the measured force from the target force was $3.5 \pm 2.6\%$. No sex differences were observed. It seemed, therefore, justifiable to pool the data for men and women.

Figures 5, 6 and 7 show the mean and s.d. results for all motor tasks and all experimental sessions. No significant (P > 0.05) activity differences among the sessions were observed for identical MB tasks with the exception of MB in IC in the T2' sequence. In that case, significant (P < 0.05) reduction in the activity was observed compared with all other repetition sequences (Fig. 6).

When performing unilateral and bilateral CT, significant (P < 0.01) reduction in the EMG activity between the first and the third experimental sessions for all bite force levels except 50 N was observed for the masseter and temporal muscles. Depending on the muscle and the repetition sequence (T3 or T3'), the EMG decrease ranged from 32 to 44%. The repetition sequences within sessions 2 (T2, T2') and 3 (T3, T3') revealed no significant (P > 0.05) activity changes. Between the first and second sessions, the activity decline ranged from 15% to 34%. However, this effect was not consistently significant for all muscles and all forces (Fig. 5).

No significant differences between integrated activity in the sessions were observed for chewing tasks (Fig. 7).

^{‡‡}SPSS Inc., Chicago, IL, USA.



Fig. 5. EMG activity of the muscles monitored, averaged over the three replicates of the different coordination tasks (CT). The three sessions are denoted T1, T2, and T3; additional sequences in the follow-up sessions are denoted T2' and T3'. Asterisks show significant (P < 0.05) differences between T1 and the follow-up sessions T2/T2', T3/T3'; u50 to u300 = unilateral CT, b50 to b300 = bilateral CT, both with bite forces of 50, 100, 200, and 300 N.

Discussion

The main result of our investigation was the finding that jaw muscles are remarkably prone to motor adaptation when CT must be accomplished. One single training session with feedback-guided balancing tasks at baseline (with 24 replicates of the CT) reduced overall EMG activity by approximately 20% in a follow-up 2 weeks post-baseline. Another reduction in approximately 20% was observed from the second to third sessions 10 weeks post-baseline after two training sequences during the second session. Extended within-session replicates (sequences T2' and T3') revealed no immediately measurable effects on motor behaviour, however. The EMG values revealed no significant training effects for either MB tasks or chewing in the 10-week period.

These results are only partly comparable with those from previous studies of the oro-facial region, in particular, the explicit tongue-task training recently reported (29). The training pattern in our study used synchronously implicit and explicit training components (12). It is supposed that the applied balancing task provoked the motor system to use, unconsciously, the intrinsic cocontraction repertoire to adjust static equilibrium, i.e. this strategy was the implicit component of the motor tasks. In contrast, the feedback-guided force control constituted the explicit part of the training pattern. This might possibly explain the long-term motor adaptation in our study without daily sessions over a period of a week, as has been reported for tongue-task training. In addition, the coordination training was embedded in two sequences of motor activity, which represented established motor strategies. It is possible that these additional components had a stabilising or enhancing effect on long-term retention. Future studies will have to elucidate the basis of the remarkable long-term retention of the training effects observed in this study.

Typically, experimental designs use a variety of measures of performance for motor learning, for example reaction times, velocity changes, kinematic precision and force output. In contrast, this investigation evaluated overall behavioural motor changes on the basis of EMG recordings of the masticatory muscles only. It might be argued that an absolute decline in the EMG activity may not be inferred from the data obtained, because intra-muscular and/or intermuscular activity rotation or substitution of active motor unit populations (18) may be responsible for the reduced electric activity measured at the particular electrode sites. In principle, this objection might possibly apply to the observed reduction in approximately 20% between the first and second sessions. As an essential



Fig. 6. EMG activity of the muscles monitored, averaged over the three replicates of the maximum biting tasks. The three sessions are denoted T1, T2, and T3; additional sequences in the follow-up sessions are denoted T2' and T3'. Asterisks show significant (P < 0.05) differences between T2' and T1, T2, T3, and T3' in IC. IC = intercuspation, BCR = bilateral biting on cotton rolls, UCR = unilateral biting on cotton rolls.

prerequisite for such an effect, however, the activity decline has to be linked to fatiguing exercises (18) or robust changes in bite force direction (23, 30), neither of which occurred in this study. For the 40% activity reduction in the third session, this objection seems to be completely unrealistic, because the biomechanical advantage of the particular muscles (i.e. their lines of action) contradicts an activity reduction in this magnitude by substitution patterns or intra-muscular activity shifts when the motor system concurrently generates identical bite forces (without changes of jaw position), such as were performed in the first session. It might also be argued that the reduction in the EMG activity of the masseter and temporalis might be initiated by the synchronous activity reduction in cocontracting antagonists. In a recent study (31), for instance, participants performed a curl (weight lifting task consisting of just 10 repetitions) in which the EMG activity of both biceps and triceps was simultaneously reduced as the task was performed more efficiently. Because we investigated masseter and temporalis exclusively, data for the activity of the antagonists are not available. On the basis of investigations with varying forces and force directions (30), however, it seems unlikely that the EMG reduction in

the masseter and temporalis is enhanced by reduction in the weak cocontraction of the digastric and lateral pterygoid muscles [during vertical biting, the computed forces of both muscles are noticeably below 5% of the actual bite force (30)]. Likewise, the objection that different jaw separations (changes between 4 and 6 mm depending on the applied bite force) might be responsible for the activity changes is implausible, because identical bite forces, i.e. identical jaw separations, were compared.

According to the 'task group' hypothesis (32), the most realistic explanation of the observed phenomenon seems to be that motor units of the individual muscles with the best-fitting mechanical advantage were gradually coactivated. This optimising recruitment strategy may subsequently have reduced the initially redundant activation patterns (i.e. the initially higher EMG output) by switching off redundant motor units. This hypothesis is in good agreement with the heterogeneous or differential activation capability of the masticatory muscles, which has often been reported (33–35). As a clinical implication of this consideration, it might be speculated that the above-mentioned strategy might also help to unload painful muscle regions (i.e. motor units), because it seems plausible that the motor control



Fig. 7. Integrated EMG activity of the muscles monitored, averaged over the three replicates of the chewing tasks. The three sessions are denoted T1, T2', and T3; additional sequences in the followup sessions are denoted T2' and T3'. TR, right temporalis; MR, right masseter; TL, left temporalis; ML, left masseter.

will establish recruitment patterns that not only fit biomechanically but also cause less or no pain during loading. Whether the detected training effects will also affect the motor unit recruitment pattern of established motor tasks, for example isometric biting and chewing, remains an open question, however. Future clinical investigations must address this issue. The finding that no gain of motor adaptation within a session could be observed is indicative of a relatively fast saturation effect of the training pattern used and supports the idea that it is not the number of replicates in an initial session but rather the saturation of the performancerelevant variables that predicts a delayed performance gain (36).

The MB tasks revealed no essential changes of the EMG activity among the three sessions with the exception of MB in IC, for which a significant decrease in activity was observed in the second sequence (T2') of session 2. The overall reduction in muscle EMG activity may, rather, be explained as a transient avoidance pattern triggered by periodontal nociceptors (it must be recognised that MB is not a common physiological task and may induce painful perceptions) rather than a motor adaptation effect. This idea is supported by the fact that the immediately following tasks on cotton rolls

did not repeat this effect and that the decrement disappeared completely in the third session in both T3 and T3'. This finding has an additional implication for clinical EMG experiments. MB in IC is used to obtain data for normalisation of submaximum muscle activity. Considering the results reported, it seems advantageous to obtain MB records with cotton rolls between the tooth rows, as has previously been recommended (37), because these data were indicative of a consistent level of activity over all sessions.

For chewing tasks, there were no significant EMG activity changes with regard to the integrated data. The results for standardised chewing were only compared on the basis of 'energy consumption' during chewing. Chewing test food might also have the character of a novel task, however. It is therefore possible that other variables, for example burst duration, occlusal time and chewing velocity, have changed. Future studies must address this issue.

Nevertheless, MB tasks on cotton rolls and test food chewing, both of which lack long-term motor adaptations with regard to EMG recordings, might be recommended for clinical follow-up evaluations of function in patients with TMD.

In conclusion, this study showed that the masticatory muscles are remarkably prone to motor adaptation if demanding CT must be accomplished. Force-controlled balancing tasks seem to be a promising tool to train masticatory muscles, with long-term adaptation. Future studies will have to test whether this effect is of therapeutic relevance.

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References

- Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT. Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. Brain. 1996;119(Pt 4):1199–1211.
- Bastian AJ. Understanding sensorimotor adaptation and learning for rehabilitation. Curr Opin Neurol. 2008;21:628–633.
- 3. Carson RG. Changes in muscle coordination with training. J Appl Physiol. 2006;101:1506–1513.
- Dishman RK, Berthoud HR, Booth FW, Cotman CW, Edgerton VR, Fleshner MR *et al.* Neurobiology of exercise. Obesity (Silver Spring). 2006;14:345–356.

- Zehr EP. Training-induced adaptive plasticity in human somatosensory reflex pathways. J Appl Physiol. 2006;101: 1783–1794.
- 6. Carson RG, Riek S. Changes in muscle recruitment patterns during skill acquisition. Exp Brain Res. 2001;138:71–87.
- Shemmell J, Tresilian JR, Riek S, Barry BK, Carson RG. Neuromuscular adaptation during skill acquisition on a two degree-of-freedom target-acquisition task: dynamic movement. J Neurophysiol. 2005;94:3058–3068.
- Shemmell J, Forner M, Tresilian JR, Riek S, Barry BK, Carson RG. Neuromuscular adaptation during skill acquisition on a two degree-of-freedom target-acquisition task: isometric torque production. J Neurophysiol. 2005;94:3046–3057.
- 9. Lotze M, Braun C, Birbaumer N, Anders S, Cohen LG. Motor learning elicited by voluntary drive. Brain. 2003;126:866– 872.
- Muellbacher W, Ziemann U, Boroojerdi B, Cohen L, Hallett M. Role of the human motor cortex in rapid motor learning. Exp Brain Res. 2001;136:431–438.
- Duchateau J, Semmler JG, Enoka RM. Training adaptations in the behavior of human motor units. J Appl Physiol. 2006;101:1766–1775.
- Siengsukon CF, Boyd LA. Does sleep promote motor learning? Implications for physical rehabilitation. Phys Ther. 2009;89:370–383.
- Forrester LW, Wheaton LA, Luft AR. Exercise-mediated locomotor recovery and lower-limb neuroplasticity after stroke. J Rehabil Res Dev. 2008;45:205–220.
- Hayden JA, van Tulder MW, Tomlinson G. Systematic review: strategies for using exercise therapy to improve outcomes in chronic low back pain. Ann Intern Med. 2005;142:776–785.
- 15. Sjogaard G, Sogaard K. Muscle injury in repetitive motion disorders. Clin Orthop Relat Res. 1998;351:21–31.
- Hägg GM. Static work and myalgia a new explanation model. In: Andersson PA, Hobart DJ, Danoff JV, eds. Electromyographical kinesiology. Amsterdam: Elsevier Science, 1991:141–144.
- Mense S, Simons DG. Muscle pain: understanding its nature, diagnosis, and treatment. Philadelphia: Lippincott Williams & Wilkins, 2001:253–259.
- Farella M, Palumbo A, Milani S, Avecone S, Gallo LM, Michelotti A. Synergist coactivation and substitution pattern of the human masseter and temporalis muscles during sustained static contractions. Clin Neurophysiol. 2009;120: 190–197.
- Schindler HJ, Rues S, Türp JC, Lenz J. Heterogeneous activation of the medial pterygoid muscle during simulated clenching. Arch Oral Biol. 2006;51:498–504.
- Turkawski SJ, Van Eijden TM, Weijs WA. Force vectors of single motor units in a multipennate muscle. J Dent Res. 1998;77:1823–1831.
- Blanksma NG, van Eijden TM. Electromyographic heterogeneity in the human temporalis and masseter muscles during static biting, open/close excursions, and chewing. J Dent Res. 1995;74:1318–1327.
- 22. Phanachet I, Whittle T, Wanigaratne K, Klineberg IJ, Sessle BJ, Murray GM. Functional heterogeneity in the superior

head of the human lateral pterygoid. J Dent Res. 2003;82:106–111.

- 23. Schindler HJ, Türp JC, Blaser R, Lenz J. Differential activity patterns in the masseter muscle under simulated clenching and grinding forces. J Oral Rehabil. 2005;32:552–563.
- 24. Svensson P, Romaniello A, Wang K, Arendt-Nielsen L, Sessle BJ. One hour of tongue-task training is associated with plasticity in corticomotor control of the human tongue musculature. Exp Brain Res. 2006;173:165–173.
- Boudreau SA, Hennings K, Svensson P, Sessle BJ, Arendt-Nielsen L. The effects of training time, sensory loss and pain on human motor learning. J Oral Rehabil. 2010;37:704–718.
- Peck CC, Wirianski A, Murray GM. Jaw motor plasticity in health and disease. Comput Methods Biomech Biomed Engin. 2010;13:455–458.
- Pröschel P, Morneburg T, Hugger A, Kordass B, Ottl P, Niedermeier W *et al.* Articulator-related registration–a simple concept for minimizing eccentric occlusal errors in the articulator. Int J Prosthodont. 2002;15:289–294.
- Slagter AP, Bosman F, Van der Bilt A. Comminution of two artificial test foods by dentate and edentulous subjects. J Oral Rehabil. 1993;20:159–176.
- Boudreau SA, Farina D, Falla D. The role of motor learning and neuroplasticity in designing rehabilitation approaches for musculoskeletal pain disorders. Man Ther. 2010;15:410–414.
- Schindler HJ, Rues S, Türp JC, Schweizerhof K, Lenz J. Jaw clenching: muscle and joint forces, optimization strategies. J Dent Res. 2007;86:843–847.
- Vance J, Wulf G, Tollner T, McNevin N, Mercer J. EMG activity as a function of the performer's focus of attention. J Mot Behav. 2004;36:450–459.
- 32. Loeb GE. Motoneurone task groups: coping with kinematic heterogeneity. J Exp Biol. 1985;115:137–146.
- 33. Blanksma NG, van Eijden TM, van Ruijven LJ, Weijs WA. Electromyographic heterogeneity in the human temporalis and masseter muscles during dynamic tasks guided by visual feedback. J Dent Res. 1997;76:542–551.
- Türp JC, Schindler HJ, Pritsch M, Rong Q. Antero-posterior activity changes in the superficial masseter muscle after exposure to experimental pain. Eur J Oral Sci. 2002;110:83–91.
- Farella M, Van Eijden TMGJ, Baccini M, Michelotti A. Task related electromyographic spectral changes in the human masseter and temporal muscles. Eur J Oral Sci. 2002;110:8–12.
- Hauptmann B, Reinhart E, Brandt SA, Karni A. The predictive value of the leveling off of within session performance for procedural memory consolidation. Brain Res Cogn Brain Res. 2005;24:181–189.
- 37. Ferrario VF, Tartaglia GM, Galletta A, Grassi GP, Sforza C. The influence of occlusion on jaw and neck muscle activity: a surface EMG study in healthy young adults. J Oral Rehabil. 2006;33:341–348.

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