

DIGASTRIC MUSCLE RESPONSE AS A FUNCTION OF KNOWLEDGE OF THE TASK TO BE PERFORMED

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Summary—Whether the motor programme executed by the digastric muscles during a forceful bite is modified according to a subject's expectation that the resistance between the teeth will change was investigated. There were two experimental conditions: (1) tracking a ramp (drawn on an oscilloscope screen) by biting (isometrically) on a force transducer and holding it at 120 N, and (2) tracking the same ramp with a sudden unloading at 100 N. There were two groups of experiments: (1) control experiments in which subjects underwent a sudden and unexpected unloading of the jaw, and (2) experiments in which subjects were previously informed whether or not there was to be an unloading. In all experiments the subjects co-contracted their digastric muscles during the bite as compared to the state at rest. The subjects' responses fell into the three different types: (i) those who varied the level of tonic digastric activity only as a function of the experimental condition, (ii) those who co-contracted the digastric muscles at the same time as the masseter muscles, and (iii) those who changed the contraction pattern of the digastric muscles as a function of the experimental condition. If modulation of the digastric muscles occurred this is a 'feedforward' strategy mainly based on immediate past performance.

Key words: motor skill, jaw, digastric muscle, human, learning, anticipation, mastication.

INTRODUCTION

Hannam, Matthews and Yemm (1968) showed that when the resistance to a forceful isometric bite is suddenly withdrawn, the jaw-closing movement is arrested before the teeth come together. In this condition an unloading reflex (inhibition of jaw-closing and excitation of jaw-opening muscles) is evoked. According to Miles and Wilkinson (1982), the inhibition of the jaw-closing muscles and the reflex activation of the jaw-opening muscles occurs too late to explain the rapid arrest of mandibular movement; jaw-opening and jaw-closing muscles co-contract during the bite. They suggested that the stiffness resulting from the co-contraction of jaw-opening muscles during biting is the mechanism responsible for preventing the teeth snapping together when the resistance is withdrawn.

Miles and Madigan (1983) looked deeper into this matter and investigated whether the motor programme executed by the digastric muscles is modified according to the subject's expectation of whether or not the jaw closing yields. They showed that, when unloading is expected, some subjects co-activate their digastric muscles either tonically during the entire bite, or phasically at a specific threshold of net closing force. They suggested the possibility of past experience as a source for the modification of the jaw-opening muscles.

To investigate the latter possibility we have now studied whether changes in the pattern of co-activation of the opening muscles depend:

- (1) upon foreknowledge of the task to be performed,
- or
- (2) upon the immediate past performance of the task executed.

We asked these questions because Ottenhoff *et al.* (1992) reported that, although the muscle activity generated to overcome the resistance of food is mainly triggered peripherally, anticipatory mechanisms are present which generate additional muscle activity before the onset of force during chewing.

In most of the experiments subjects were asked to carry out a controlled isometric bite knowing whether the resistance between the teeth would yield a known force or not. We compared the outcome with initial experiments in which the subjects—still being uninformed—underwent a sudden and unexpected decrease in resistance between their teeth.

MATERIALS AND METHODS

Eighteen dentate subjects (10 in England and eight in The Netherlands) participated in the experiments. All were free from signs of muscular or temporomandibular dysfunction.

Throughout the experiments the subjects sat in front of a device (Fig. 1) which could be used either

Abbreviations: EMG, electromyogram, -graphic; IPSP, inhibitory postsynaptic potential.

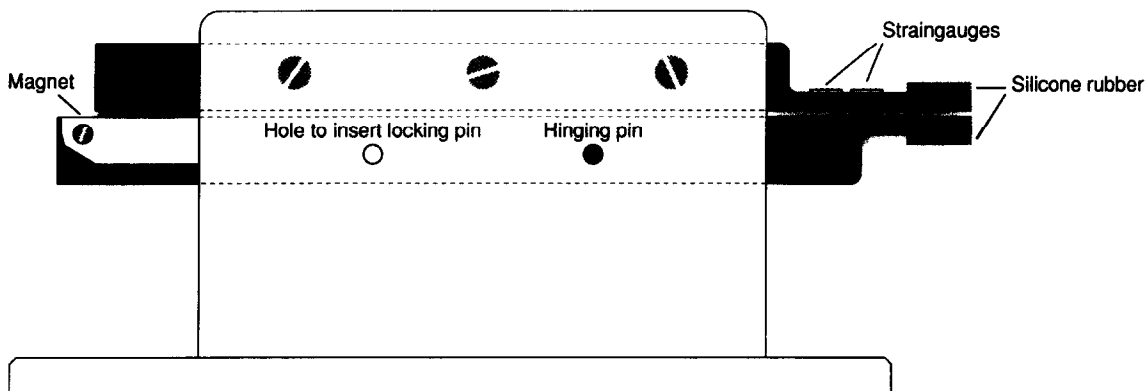


Fig. 1. Apparatus used as a simple force transducer or as an 'unloading' apparatus: two parallel stainless-steel bars are attached to two metal plates mounted on a heavy support; the lower bar either hinges around a pin (unloading mode) or is locked by inserting an additional pin in a hole provided (force transducer mode); the initial resistance to closing is achieved by a magnet between the upper and lower bar.

as a simple force transducer or as an 'unloading' apparatus. The apparatus was adjusted so that it was at the level of the mouth. Bite forces were exerted between the upper and lower incisors and cuspids. Behind the apparatus the subject could see the magnitude of the exerted bite force displayed on an oscilloscope monitor. An oblique line was drawn on this monitor screen.

The apparatus contained two parallel stainless-steel bars, 80 mm long, 50 mm wide and 6 mm thick. For comfort, the area of impact of each bar was covered with a sheet of silicone rubber. The distance between the bars was 2 mm so that the subject's teeth were about 15 mm apart when biting on the device. The upper bar was attached to two vertical metal plates mounted on a heavy support. The lower bar either hinged around a pin (unloading mode) or was locked by inserting an additional pin in a hole provided (force transducer mode). The initial resistance to closing was achieved by a magnet between the upper and lower bar. A screen prevented the subject from seeing the position of the hinge or the locking pins.

Two pairs of balanced strain gauges were attached 20 mm apart on either side of the upper bar of the force transducer at 25 mm from the mouth piece. In this way the difference in torque induced by the bite force could be recorded over a fixed distance, and the bite force was measured independently of the point of force impact. The output of the force transducer was fed into a differential amplifier whose output was displayed as a dot on the monitor oscilloscope mentioned. The dot moved with a velocity of 1 division/s ($= 10 \text{ mm/s}$).

In England, the vertical movement of the lower bar relative to the upper one was also recorded by means of an axial accelerometer (Single Axis accelerometer 4373 Brüel and Kjær). Latencies were calculated by reference to the accelerometer output.

Surface EMGs were recorded from the right masseter and digastric muscles using pairs of 10-mm disc electrodes (Dutch experiments) or Dantec 13L20 silver/silver chloride electrodes (British experiments) placed at an interelectrode distance of approx. 10 mm in line with the muscle fibres of the masseter muscle, and 10–25 mm behind the mandibular insertion of the

anterior digastric muscle. The reference electrode was placed on the neck.

EMG recordings were from DC to 5 kHz. EMG signals and the output of the force transducer were all recorded on magnetic tape (1 V peak to peak). For analysis the EMGs and the force recordings were digitized (sample frequency 1 kHz). Then the digitized EMGs were rectified and averaged (bin averaging; 50 samples per bin = 50 ms) and, together with the force signal, displayed as 'tile plots'.

During the experiments a subject sat in front of the oscilloscope screen and was asked to track the ramp as drawn on the screen by biting on the two bars.

There were two experimental conditions:

- (1) tracking the ramp and holding it at 120 N, and
- (2) tracking the ramp with a sudden unloading at 100 N.

The slope of the oblique part of the ramp was such that each biting trial took 3.6 s for the British subjects and 6.0 s for the Dutch subjects.

All subjects participated in two groups of experiments. The first group comprised the control experiments in which the subjects had no knowledge of the experimental conditions. Uninformed subjects were asked to bite the ramp and hold it for a few seconds. This was repeated five times. Then between the fifth and sixth trial the apparatus was unlocked and the (still uninformed) subjects underwent a sudden and unexpected unloading of the jaw. Thereafter the subjects were told whether the apparatus was set in a locked or an unlocked mode.

In the second group of experiments the subjects had knowledge of the experimental conditions. Firstly, they were asked to track five times with the expectation of unloading at 100 N, then to bite five 'ramp and holds' with the lower bar locked, and finally, to track 10 (or six in England) times but were left uncertain about the actual experimental condition.

RESULTS

In all experimental conditions—the uninformed as well as the informed—all subjects co-contracted their

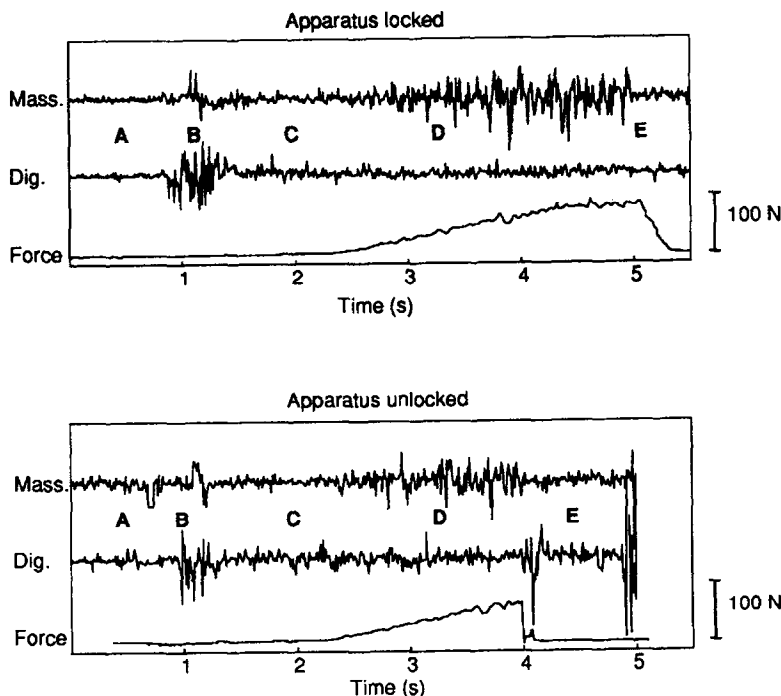


Fig. 2. EMG recording of the masseter muscle, the digastric muscle and the force of subject AM tracking a ramp on an oscilloscope screen by biting on the apparatus as shown in Fig. 1. Top figure: recordings when the apparatus was locked; bottom figure: recordings when the apparatus was unlocked and the uninformed subject underwent a sudden and unexpected unloading of the jaw. In both experimental conditions the subject co-contracted the digastric muscles during the bite as compared to 'at rest' (sections A). During sections B the subject opened the mouth, made contact with the bars of the force transducer and co-contracted the digastric muscle in anticipation to the task to be performed (sections C). Then the subject increased the biting force according to the tracking task to be performed (sections D).

digastric muscles during the bite above their 'resting' (baseline) activity (Fig. 2, sections A). In general the subjects showed the following behaviour: they opened the mouth and made contact with the bars of the force transducer (Fig. 2, sections B) and then co-contracted their digastric muscles in anticipation of the task to be performed (Fig. 2, sections C). Then, when the dot on the monitor oscilloscope appeared, they increased their biting force according to the tracking task (Fig. 2, sections D). Although this was a consistent observation, the subjects showed such great variation in the strategies applied that pooling of data did not appear possible. We therefore illustrate the outcome of our experiments for single subjects.

Examples of typical behaviour are shown in the Figs 3–5, which are 'tile plots' of the results of the subjects JB, LK, AM. In each figure the first row displays the controls. The first 'tile' is a recording of the uninformed subject who performs a 'ramp and hold' trial, the second tile shows the situation when the same uninformed subject underwent a sudden and unexpected unloading of his jaw. The second row shows recordings of a sequence of five trials of the same subject when expecting an unloading at 100 N. The third row displays five trials when the subject was assured that the apparatus was locked, whereas the fourth and the fifth row shows the 10 trials when the subject was left uncertain as to whether there was an unloading or not.

In general it appeared that:

- (1) The accuracy with which the subjects managed to track the ramp was variable from subject to subject and from trial to trial.
- (2) To cushion the shock evoked by the unloading, three types of strategies could be discerned:
 - (I) Half the subjects (9 out of the 18 studied) varied the level of tonic digastric activity only as a function of the various experimental conditions (Fig. 3).
 - (II) Others ($n = 4$) co-contracted the digastric muscles in parallel with the masseter muscles (Fig. 4).
 - (III) The third group of subjects ($n = 5$) developed anticipatory strategies by changing the contraction pattern of the jaw-opening muscles as a function of the experimental conditions (Fig. 5).

In the latter group, previous experience, knowledge of the task to be executed and immediate past performance all contributed to the anticipatory strategies. However, subjects adjusted the contraction pattern of the digastric muscles generally on the basis of the immediate past performance. When a definite anticipatory motor programme was developed, it did so within two or three trials.

- (3) After unloading, the masseter muscle remained active for 10–20 ms; thereafter it fell silent. The digastric muscles frequently maintained their activity for another 40–60 ms; a reflex burst was occasionally seen (latency 20–40 ms).

Control experiments

As mentioned before, all subjects increased the activity of the digastric muscle above the EMG level at rest during the isometric bite. Subject JB (Fig. 3) and AM (Fig. 5) co-contracted the digastric muscle tonically during the bite whereas subject LK (Fig. 4) increased the digastric activity in line with the masseter muscle.

Our subjects had difficulty in tracking the ramp smoothly; with increasing levels of bite force they were able to keep close to the track for only a short time. The subjects often lost the target and had to tune in at the target line again. The overshoots had a base frequency of about 4 Hz.

As expected, when the apparatus was secretly unlocked and the uninformed subjects experienced a sudden and unexpected unloading of the mandible, they did not change the contraction pattern of the masseter and digastric muscles in the isometric phase of the trial (Fig. 2 sections 'A'–'D'). After the unloading (sections 'E'), however, the digastric muscles remained active for another 40–60 ms, after which a reflex burst was seen. The masseter muscle remained active for 10–20 ms following unloading, after which a silent period invariably occurred.

Experiments with foreknowledge

The second rows of the Figs 3–5 show the contraction patterns of the masseter and the digastric muscles when the subjects were tracking five times with an expected unloading at 100 N. Subject JB and LK (Figs 3 and 4) did not change the activity of the muscles under study as compared to the 'naive' (uninformed) situation; JB still co-contracted the digastric muscle tonically throughout the bite whereas subject LK increased the digastric amplitude in line with the masseter muscle.

Only subject AM (Fig. 5) changed the co-contraction strategy as a function of the number of trials. In the first trial this subject applied the same strategy as when uninformed. In the second trial the subject anticipated by co-contracting the digastric muscles strongly at the beginning of the tracking, while towards the end of the task their contraction decreased. Obviously, this is not a successful strategy for intercepting the sudden unloading of the jaw, and from the third trial on our subject found the right strategy—co-contracting in line with the masseter muscle at the end of the tracking task.

Thereafter the subjects were asked to perform a 'ramp and hold' bite with the apparatus locked with the pins. The subjects were fully informed. The third rows of Figs 3–5 shows the results. Again only subject AM changed the pattern of contraction of the digastric muscles; within five 'ramp and hold' bites this subject returned to a behaviour similar to that in the uninformed condition. Attention is drawn to the gradual shift in contraction pattern of the digastric

muscles. Moreover, the first trial in this set of experiments resembles the last trial in the 'unloading' condition. In the third trial the subject was still anticipating, at about 100 N, an unloading of the jaw-closing muscles that did not occur.

In the final test our subjects were asked to track 10 times but were left uncertain as to whether the apparatus would unload or not. The fourth and the fifth rows of Figs 3–5 show the results. In this condition, subjects LB and LK (Figs 3 and 4) showed a behaviour similar to those in the other experiment whereas subject AM (Fig. 5) always co-activated the digastric muscles in line with the contracting masseter muscles, as in the 'unlocked' condition. This subject apparently 'plays it safe' as can be seen from the anticipatory reduction in force at the expected 100 N level when the apparatus was locked (uncertain, locked 2 and uncertain, locked 9). Moreover, in this condition, the subject always diminished the level of co-contraction of the digastric muscles after unloading.

After unloading, the digastric frequently kept its activity for another 40–60 ms; a reflex burst was seen in 65% of the trials (latency 20–40 ms; mean: 32 ± 12 ms); only one of the 18 subjects studied did not present a digastric burst in any of the experimental conditions. In all subjects the masseter muscle remained active for 10–20 ms after the unloading; thereafter a silent period occurred.

DISCUSSION

In general, our subjects did not perform well in tracking a ramp with their jaws under isometric circumstances. This is in line with our previous observations that a mechanism controlling bite is not well developed in the trigeminal system (Van Willigen, Broekhuijsen and Van der Meer, 1987; Van Willigen *et al.*, 1992), and those of Van Steenberghe *et al.* (1991), who showed that the capacity to maintain an isometric force under visual feedback is poorer in the jaw than in the limb.

Our first observation on the pattern of digastric activity was that all uninformed subjects co-activated these muscles during the isometric phase of the experiments. This observation is in contrast to that of Miles and Wilkinson (1982), who reported that subjects only co-contracted their digastric muscles when they anticipated that the resistance between their teeth would change. According to Miles and Wilkinson, and Otten (1991), co-contraction of the digastric muscles during a forceful bite provides the jaw system with a mechanism for dealing with unexpected events. When the mandible is suddenly accelerated as in the unloading experiments the active digastric muscles are stretched and increase their force due to the force–velocity relation of the muscle. This force is built up with the same time constant as the formation of cross-bridges and is therefore much quicker than any nervous control loop (Otten, 1991). It is suggested that this mechanism is important because the margin of safety for damage in the jaw system is small, and the forces exerted can be high.

One can argue that the stiffness increase due to the recruitment of the digastrics is the underlying mechanism for dealing with unexpected events. However,

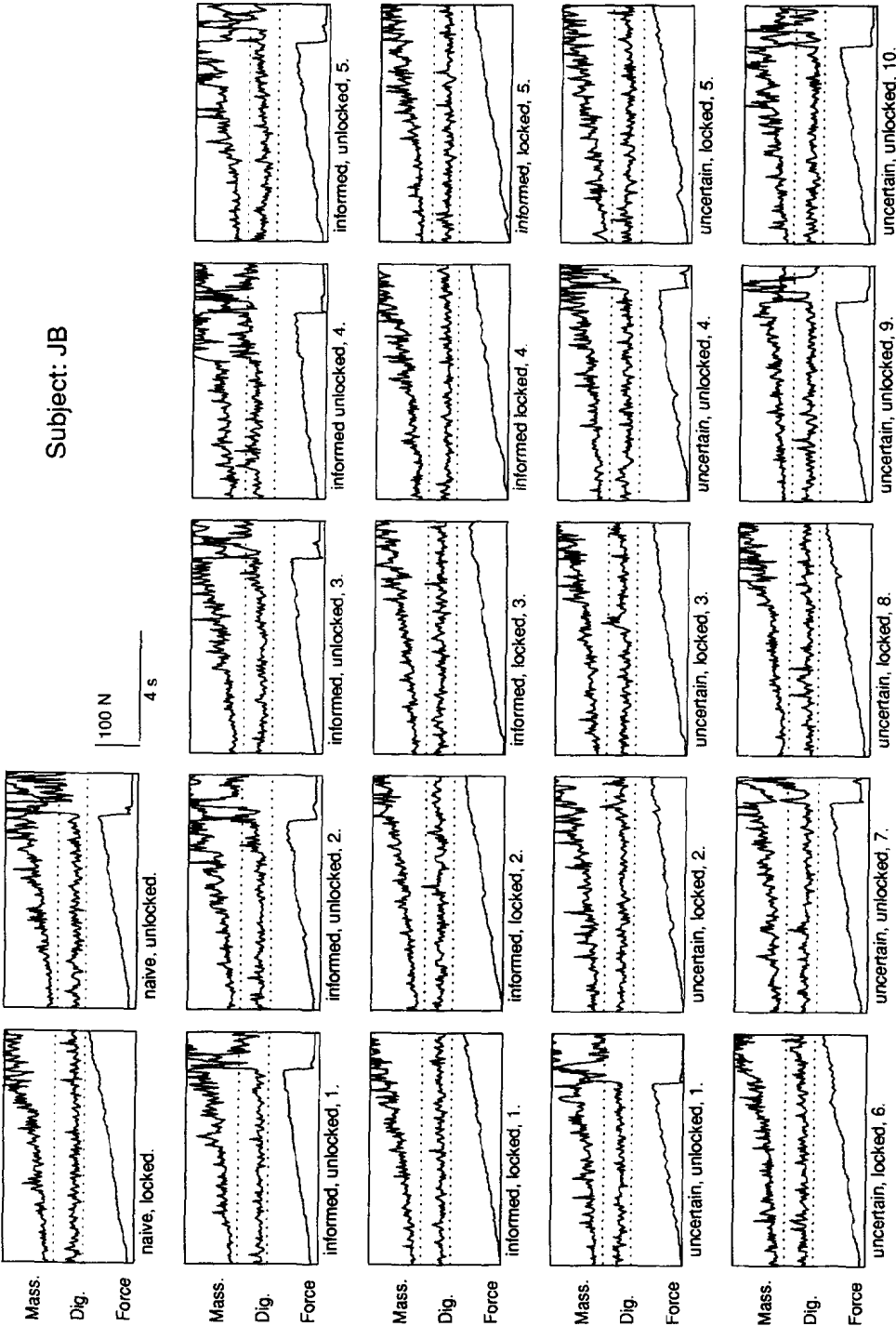


Fig. 3. 'Tile plot' of the behaviour of subject JB under different experimental conditions. In each 'tile' the upper trace displays a rectified and filtered EMG of the masseter muscle, the middle trace is the EMG of the digastric muscle and the bottom trace a recording of the force. The first row of tiles comprises recordings of the uninformed subject who performs a 'ramp and hold' trial and a recording when the same subject undergoes a sudden and unexpected unloading of his jaw. The second row shows recordings of a sequence of five trials of the same subject when expecting an unloading at 100 N. The third row displays five trials when the subject was assured that the apparatus was locked, whereas the fourth and the fifth row shows 10 trials when the subject was left uncertain whether unloading would occur or not. In all plots, the dashed lines are the base-line levels of the masseter and digastric EMGs. Note that this subject varied the level of tonic digastric activity only as a function of the various experimental conditions.

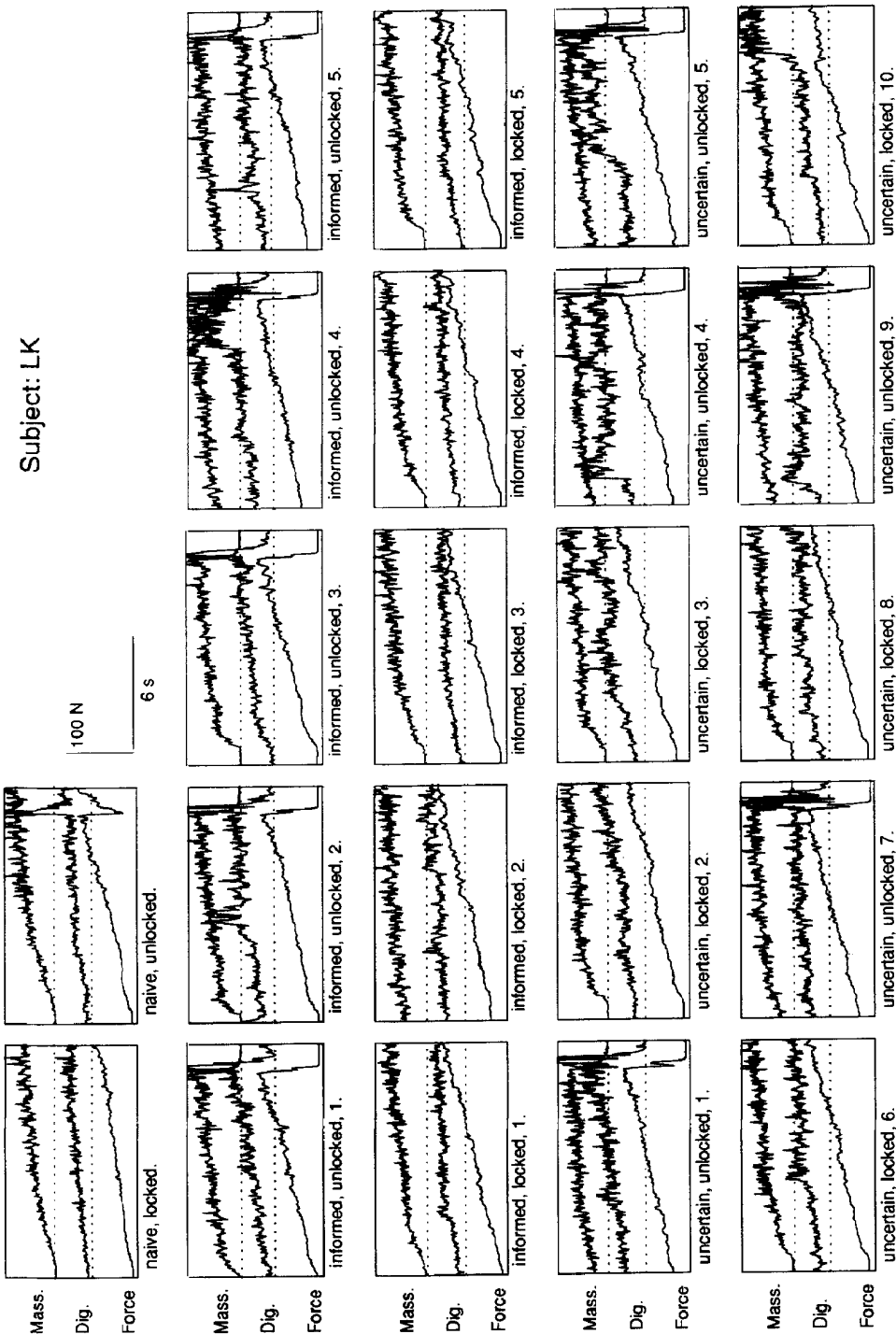


Fig. 4. 'Tile plot' of the behaviour of subject LK under the same experimental conditions as in Fig. 3. The layout of the figure is the same as in Fig. 3. This subject always co-contracted the digastric muscles in parallel with the masseter muscle. Note the different time-scale and that in the 'uncertain' condition this subject kept on biting after the apparatus snapped.

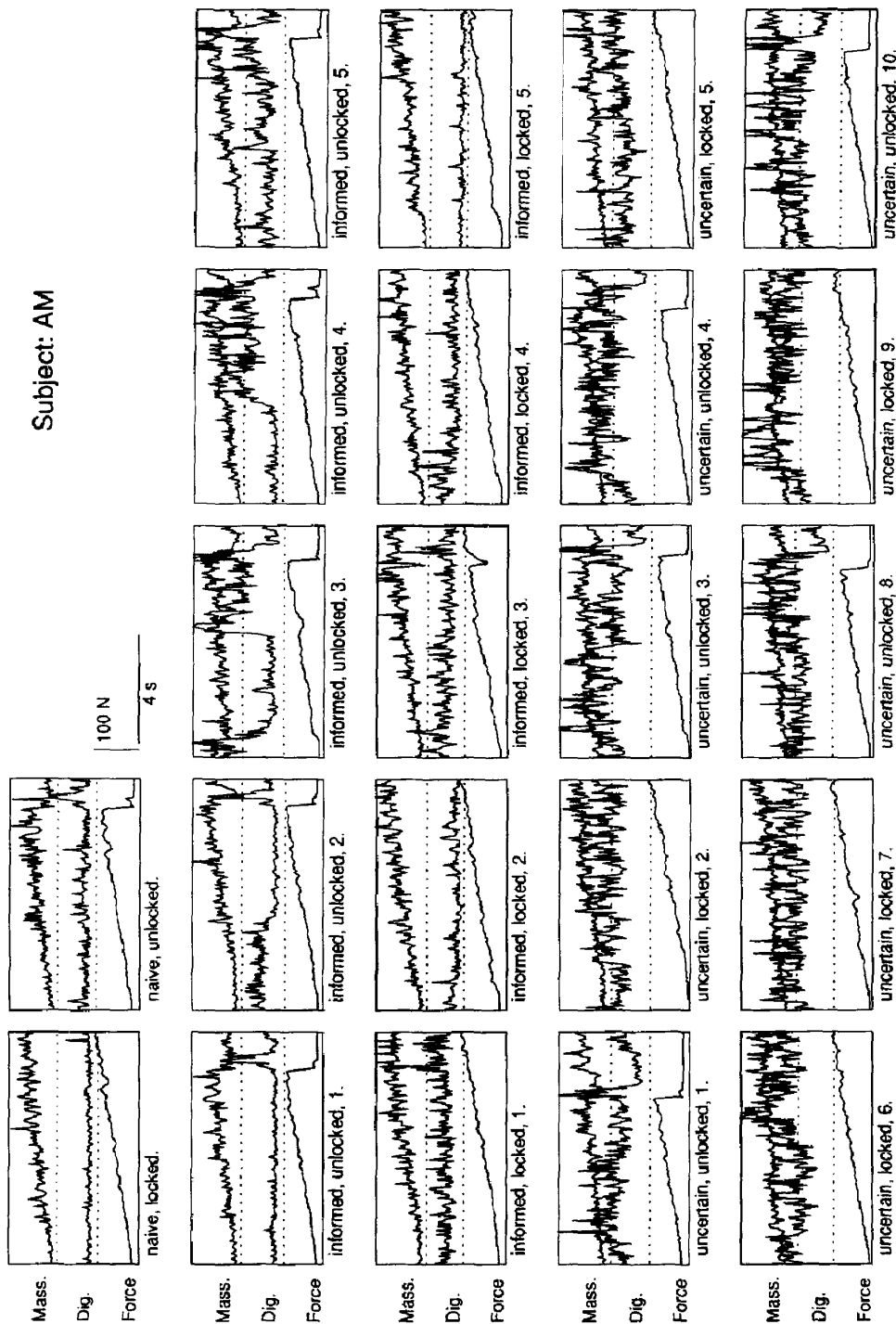


Fig. 5. 'Tile plot' of the behaviour of subject AM under the same experimental conditions as in Fig. 3. The layout of the figure is the same as in Fig. 3. This subject developed anticipatory strategies by changing the contraction pattern of the jaw-opening muscles as a function of the experimental condition. Note that the subject adjusted the contraction pattern of the digastric muscles mainly on the basis of the immediate past performance. A definite anticipatory motor programme was developed within two or three trials.

in our conditions increasing the stiffness of the jaw system by co-contraction does not help in reducing the initial build-up of the closing velocity of the jaw when the resistance between the teeth changes, as the required net bite force is independent of co-contraction. Although stiffness increases with co-contraction, it is the net force that determines the jaw acceleration. Therefore, only the reduction of the velocity-dependent muscle force can be helpful in this respect. In the case of a freely suspended lower jaw, an increase in stiffness does limit its trajectory when perturbed unexpectedly.

Our second observation on the co-contraction was that when it was known that the resistance between the teeth would change, three types of behaviour could be discerned:

Type I. Subjects (50%) who vary the level of digastric activity tonically only as a function of the various experimental conditions,

Type II. Subjects (22%) who always progressively increase the activity of the co-contracting digastric muscles in parallel with the masseter muscles.

Type III. Subjects (28%) who develop anticipatory strategies by changing the contraction pattern of the jaw-opening muscles as a function of the experimental conditions.

In this last group, previous experience, knowledge of the task to be executed and immediate past performance all contributed to the anticipatory strategies. However, subjects adjusted the contraction pattern of the digastric muscles mainly on the basis of the immediate past performance whereas a definite anticipatory motor programme was developed within two or three trials. We view these changes in the contraction pattern of the digastric muscles as an expression of learning. This is in line with the observation that in initial phases of learning a new motor skill use is made of antagonist co-contraction [for review see: Smith (1980) and Turvey, Fitch and Tuller (1982)]. It appears that the learning processes observed are fast, as in conditions of uncertainty the subject adopted a strategy that anticipated unloading from the very beginning. The anticipatory responses in digastric muscles in this group of subjects are not based on peripheral feedback, as the experiments when the subjects were uninformed show that instantaneous feedback is too late to evoke such responses. This appears to be in contrast to the findings of Ottenhoff *et al.* (1992), who showed that, during chewing, additional activity of jaw-closing muscles—generated to overcome the resistance of the food—is mainly triggered peripherally. They also reported that there are no changes in the digastric muscles when the consistency of the food is suddenly changed. We realize, however, that chewing is quite different from increasing a force isometrically and then suddenly decreasing the resistance to that force.

We suggest that in our experiments when an (informed) subject expects the resistance between the jaws to yield suddenly, the mismatch between the sensory image of the task to be executed and the result of the motor programme exerted is used to update for a better motor programme. This is a feedforward strategy. Apparently this strategy is not immediately successful; it takes a number of trials to

find the optimal motor programme. Past performance is used to update the programme.

Taylor and Cody (1974) and Goodwin and Luschei (1975) have suggested that the reduction of masseter muscle activity after unloading is caused by a dysfacilitation of the masseter motoneurons (via the stretch reflex or a transcortical arc), or an inhibition as part of a jaw-opening reflex caused by temporomandibular joint receptors or periodontal receptors. In favour of this idea is the observation that the latency of the onset of the reduction in masseter activity is more or less comparable to the latency of the monosynaptic jaw-jerk reflex.

It is implausible that periodontal receptors are primarily involved in the reduction of the activity of the masseter muscle after unloading, although Dessem, Iyadurai and Taylor (1988) show that low-threshold periodontal receptors inhibit masseter motoneurons. In our experiments, however, the level of excitation of this type of receptor is diminished when the load is suddenly released, and a resultant excitation of the masseter muscle would be expected, which is not the case.

On the other hand, it could well be that a long-lasting plateau of inhibition in the jaw-closing motoneurons is built up by the excitation of the periodontal receptors, and that when—due to the unloading of the contracting jaw-closing muscles—the drive of the shortening jaw-closing muscle spindles falls away, the jaw-closing motoneurons are left inhibited. This fits well with the observations of Cody, Harrison and Taylor (1975), Goodwin and Luschei (1975), Appenteng, Lund and Séguin (1982) and Gottlieb and Taylor (1983), who showed that activity of the fusimotor neurones of the trigeminal system is able to drive spindle afferents of the jaw-closing muscles. This would also be in line with the experiments of Kidokoro *et al.* (1968), who showed that, in the cat, a single supramaximal stimulus of the inferior alveolar nerve induces a large infused IPSPs of more than 15 ms duration in the jaw-closing motoneurons. In line with the latter observations, Minkels, Jüch and Van Willigen (1993) have shown that in the rat graded pulse stimulation of the inferior alveolar nerve induces fused IPSPs in the jaw-closing motoneurons which develop into a plateau potential of long duration (25–30 ms) and large amplitude (10–12 mV) at supramaximal intensities.

However, against this interpretation, bilateral lesions of the tract of the mesencephalic nucleus (which contains the cell bodies of the jaw-closing muscle spindles) in the monkey does not affect the unloading response when the animals eat brittle biscuits (Goodwin and Luschei, 1974), leading to the conclusion that alpha drive from jaw-closing muscle spindles is not a powerful source of excitation. This position is also taken by Lavigne *et al.* (1987), who suggest that the periodontal afferents provide a large positive feedback to the jaw-closing muscles during closure.

We have shown that subjects modulate their digastric muscles in anticipation of an expected unloading during a forceful bite. Three types of anticipatory strategies are found. If modulation of the digastric muscles occur this is a 'feedforward' strategy mainly based on immediate past performance. We think that

the decrease in masseter activity after unloading is of neural origin, whereas the sudden accelerations of the lower jaw is accounted for by co-contracting the digastric muscles.

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