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Pulsatile control of the human masticatory muscles

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Spectral analysis of jaw acceleration confirmed that the human mandible 'trembles' at a peak frequency around 6 Hz when held in its rest position and at other stationary jaw openings. The 6 Hz tremor increased during very slow movements of the mandible, but other lower-frequency peaks became prominent during more rapid jaw movements. These lower-frequency peaks are likely to be the result of asymmetries in the underlying, voluntarily produced, 'saw-tooth' movements. In comparison, finger tremor at rest and during slow voluntary movements had a mean peak frequency of about 8 Hz: this frequency did not change during rhythmical finger flexion and extension movements, but the power of the tremor increased non-linearly with the speed of the movement. The resting jaw tremor was weakly coherent with the activity of the masseter and digastric muscles at the tremor frequency in about half the subjects, but was more strongly coherent during voluntary movements in all subjects. The masseter activity was at least 150 deg out of phase with the digastric activity at the tremor frequency (and at all frequencies from 2.5–15 Hz). The alternating pattern of activity in antagonistic muscles at rest and during slow voluntary movements supports the idea that the masticatory system is subject to pulsatile control in a manner analogous to that seen in the finger.

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In a subject sitting or standing upright, the mandible is maintained in a reasonably constant vertical position with respect to the maxilla, in which the teeth remain a few millimetres apart. This posture is variously called the 'rest', 'postural' or 'habitual mandibular' position. While we use the expression 'rest position' in this report, this is not intended to imply that the jaw muscles are inactive in this posture.

It has been shown in several earlier studies that the jaw is not completely stationary in the rest position; rather, it oscillates over a very small distance in a tremor-like manner (Palla & Ash, 1979; de Vries *et al.* 1984). In a more recent study, Junge *et al.* (1998) reported that, when subjects bit weakly onto a spring-loaded position sensor near the vertical rest position, the jaw trembled at a mean power frequency of about 7 Hz. Their data indicate that this jaw tremor is not the result of cardioballistic inputs (cf. Palla & Ash, 1979) or damped mechanical vibrations; rather, their analyses indicate that the tremor has a significant neurogenic component. It may, therefore, result from the activity of a central pacemaker or from stretch reflexes in the masticatory muscles (Elble *et al.* 1987).

Tremor-like movements are seen in the limbs not only when they are stationary, but also during slow voluntary movements. Movements that are intended to be smooth are actually interspersed with regular pulses of acceleration and deceleration. These discontinuities in slow movements are the result of alternating bursts of activation of the agonist and antagonist muscles involved in the movement, a phenomenon known as 'pulsatile control' (Vallbo & Wessberg, 1993; Farmer, 1999). It has been argued that these discontinuities are the result of a different control mechanism than that which is responsible for physiological tremor.

Pulsatile control has not been widely investigated in muscles other than those controlling the fingers, and has not been reported in the trigeminal motor system. This is an important issue, because the control systems for the masticatory muscles differ in many ways from those of the fingers. In particular, the jaw-opening muscles contain few, if any, muscle spindles and there are no reciprocal inhibitory stretch reflexes between the jaw openers and closers (Luschei & Goldberg, 1981) that could participate in a pulsatile pattern of activation, or in resting tremor.

Hence, the aim of the current study was to determine whether the position of the mandible is subject to pulsatile control while in its rest position and during voluntary jaw movements. Like Junge *et al.* (1998), we have used coherence analysis to determine the relationship between

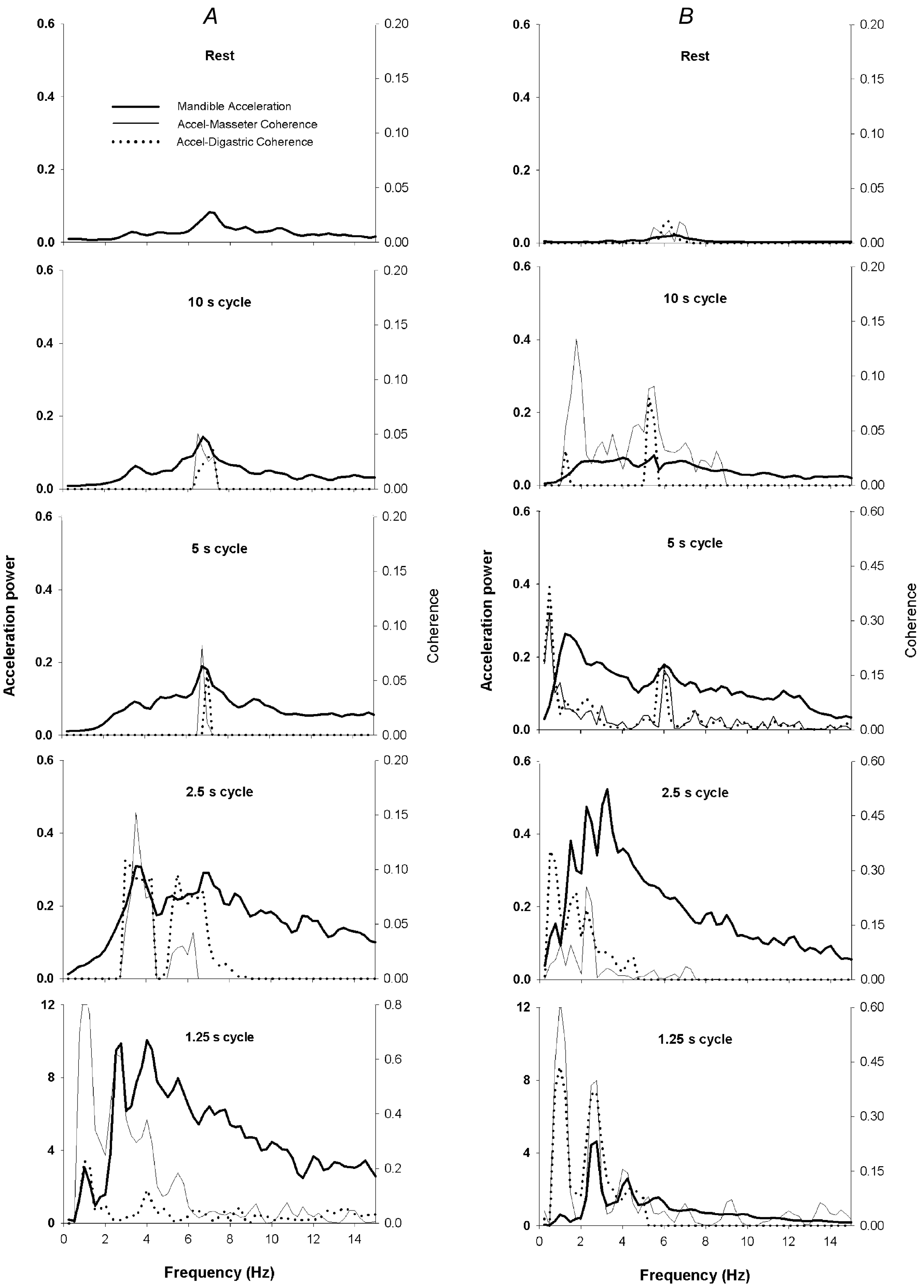

Figure 1. Coherence of masticatory muscle activity with jaw acceleration at rest and during rhythmical voluntary jaw-opening and -closing movements

The data are from two subjects (*A* and *B*) who were attempting to track a sawtooth target with cycle periods of muscle activity and jaw movement. This analysis is the frequency domain counterpart of a cross-correlation function, which relates two concurrent data streams (Rosenberg *et al.* 1998). Amongst other things, it can enable weak relationships in the frequency domain to be identified and quantified.

For simplicity, we use the expression 'tremor' to describe the regular discontinuities in position and slow movements without intending to imply that the same mechanism is responsible for both.

METHODS

The subjects (4 male, 4 female; age, 21–54 years) gave informed written consent. The subjects had no history of neurological disorders or dysfunction of the masticatory system. The experiments were approved by the Human Research Ethics Committee of Adelaide University and were consistent with the recommendations of the Declaration of Helsinki.

An accelerometer was glued to a lower incisor tooth to monitor acceleration of the mandible in the vertical plane (Flavel *et al.* 2002). This was a single-axis piezoelectric device with a linear output of 400 mV m^{-1} s^{-2} in the bandwidth DC to 5 kHz (model ADXL105Q, Analog Devices, Norwood, MA, USA). An identical accelerometer was glued to the fingernail of the right middle finger, which was splinted to keep the interphalangeal joints extended. Electrodes were placed 2 cm apart on the skin overlying the right masseter and the anterior belly of the right digastric muscle to record their surface electromyograms (EMGs).

Subjects sat comfortably in a slightly reclined position in a dental chair, with the head supported by a headrest to eliminate possible confounding effects of head tremor (Gresty & Halmagyi, 1979). They viewed an oscilloscope screen on which a horizontal target line was projected.

The jaw tremor was first measured for a 2 min epoch while the subjects were asked to sit quietly and keep their mandible at its 'normal comfortable rest position'.

Subjects were then asked to keep their jaw position at each of a series of inter-incisal separations for 2 min. These separations were established by asking the subjects to close gently onto a series of Perspex bite-blocks which separated their incisor teeth by either 10 or 20 mm, and then to keep that mandibular position when the bite-block was removed. These jaw postures were examined in random order and were separated by at least 30 s rest.

Next, subjects made a series of rhythmical jaw opening and closing movements. The horizontal target line moved at constant velocity downwards and upwards, and the subjects were asked to move their mandible at a rate that followed this 'sawtooth' target. The cycle periods were 1.25, 2.5, 5 and 10 s. Subjects were asked to keep their teeth from touching during the closing phase, and to open to a comfortable distance during the opening phase. They were given no feedback on their movement. Each run lasted for 2 min and was followed by a rest period of at least 1 min, and the four target velocities were performed in random order.

A similar protocol was followed for the finger trials, except that finger muscle EMG was not recorded. The subject's hand was supported palm-down in a custom-made splint that allowed unimpeded movement of the right middle finger. The interphalangeal joints were immobilised with a simple splint. Rest tremor was recorded with the finger relaxed in a comfortable, neutral, near-horizontal position, after which the subject was asked to make rhythmical flexion and extension movements about the metacarpophalangeal joint, tracking the same series of target velocities used for the jaw. Again, each target was given in random sequence separated by rest periods of at least 1 min.

The EMG and acceleration signals were amplified in the bandwidth DC to 0.5 kHz, and recorded on digital tape. All signals were then digitised at 2048 samples s^{-1} with a laboratory interface (1401plus, CED Ltd, Cambridge, UK).

The digitised data were then imported into Matlab version 6.0 (The Mathworks Inc., USA) where the EMG signals were full-wave rectified. All signals were low-pass filtered (zero-phase, 8th order Butterworth) to 50 Hz, and the sampling rate was then reduced to 128 samples s^{-1} for calculation of their spectral densities and the coherence, gain and phase between the EMG signals in the masticatory muscles and the acceleration records under the different experimental conditions. A single, continuous 2 min epoch of data was analysed in every case. In the calculation of coherence, values of less than 10^{-3} of the peak value were set to zero. The finger data were analysed only for spectral density.

RESULTS

Jaw tremor in the rest position

The tremor of the jaw when it was held in its rest position (i.e. with the incisor teeth separated by 2–5 mm) was not visible by eye, but appeared in the spectra as a peak centred on 6.2 ± 1.2 Hz (mean ± S.D.). Examples of the tremor spectrum derived from the jaw accelerometer in two subjects are shown as the thick lines in the uppermost panels in Fig. 1. These show a peak centred at about 7 Hz in subject A and at about 6 Hz in subject B. A resting tremor was seen in the spectra in all subjects. The spectral density of jaw tremor did not change consistently when the mandible was held voluntarily at different vertical positions (10 and 20 mm).

1.25, 2.5, 5 and 10 s (and therefore different velocities of mandibular movement). The thick lines show the spectral density measured from the accelerometer on the mandible (arbitrary units for power), the thin lines show the coherence between masseter EMG and the jaw acceleration, and the dotted lines the coherence between digastric EMG and jaw acceleration in the bandwidth 0.25–15 Hz. The lowest-frequency peaks in the spectra and coherence peaks in the lowermost panels arise from the kinetics of the rhythmical jaw movement task (1.25 s cycle time corresponds to a frequency of 0.8 Hz). Note the different vertical scaling for the lowest trace in *A*, and the three lowest traces in *B*. Values of less than 10^{-3} of the peak coherence value are set to zero.

Coherence was detected between the jaw acceleration and the activity in both masseter and digastric muscles in four of the eight subjects. The data shown in the uppermost panel of Fig. 1*A* are from a subject in whom no coherence between the tremor and the muscle activity was detected. However, in the second subject (Fig. 1*B*), the uppermost panel shows that the EMG in both masseter and digastric muscles was weakly coherent with the jaw acceleration at the peak resting tremor frequency.

When clear coherence was observed between muscle activity and the acceleration at the rest tremor frequency, the phase difference between the masseter and digastric EMG was 150–180 deg at this frequency (Fig. 2*A*). The same out-of-phase relationship was seen during the 5 s cyclical movement at the tremor frequency, and indeed at all other frequencies above 3 Hz. The decreased phase difference at the lower frequencies probably reflects the transition between opening and closing movements. This indicates that these two muscles were activated alternately rather than concurrently. Note that the coherence between the activity of both digastric and masseter muscles with jaw acceleration is much lower in the tremor frequency range when the jaw is at rest compared with when it is moving rhythmically with a 5 s cycle time.

Jaw tremor during active movements

During voluntary rhythmical jaw movements, discontinuities in both opening and closing phases were readily seen by eye at all movement speeds. However, Fig. 1 shows that the form of the spectral density of jaw acceleration changed progressively as the subjects moved their jaws at higher velocities (i.e. shorter cycle times). The overall power of the mandibular acceleration spectrum increased progressively at higher movement speeds, as expected. The peak at the tremor frequency increased at higher speeds, but additional, higher-amplitude peaks at lower frequencies emerged progressively. These peaks appear to be associated with the cycle frequency of the movement and some of its higher harmonics, suggesting distortion of the smooth cyclical movement. There was also a shift in the frequencies at which the acceleration record was coherent with both masseter and digastric muscle EMG.

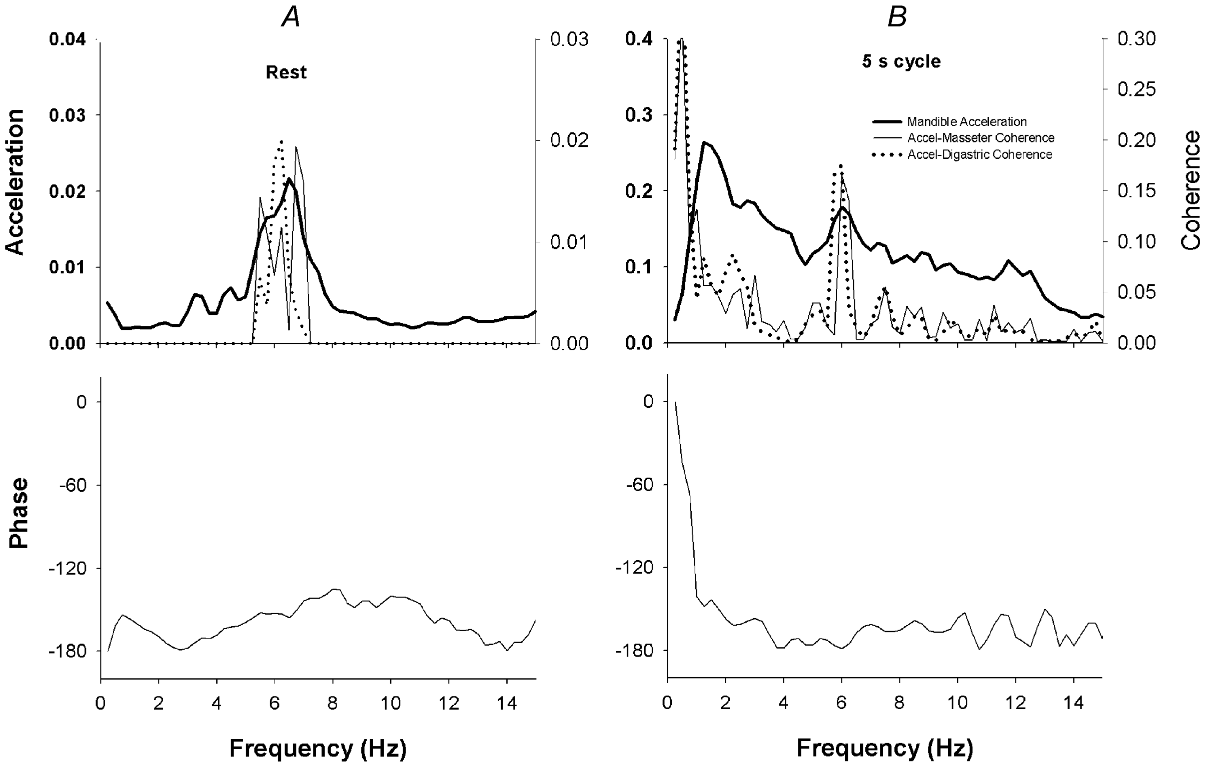

Figure 2. Phase relationship between antagonistic masticatory muscles at rest and during rhythmical jaw movements

Records obtained at rest are shown in *A*, and the records obtained during rhythmical opening and closing movements with a cycle time of 5 s are shown in *B*. The upper traces are reproduced from Fig. 1 at higher gain to show the spectrum of the mandibular acceleration at rest and the coherence between the mandibular acceleration and the masseter (thin lines) and between the mandibular acceleration and digastric muscle (dotted lines). Below these traces is a plot of the phase between the masseter EMG and the digastric EMG across the bandwidth 0.25–15 Hz. (Frequencies < 0.25 Hz are truncated for reasons of scaling). Coherence values of less than 10^{-3} peak coherence are set to zero.

When subject A held his mandible quietly in the rest position, the spectrum was dominated by a broad tremor peak centred around 7 Hz and a smaller peak at about 3.5 Hz which were not coherent with masseter or digastric muscle activity. During the very slow movements (10 s and 5 s cycle times), both peaks increased in amplitude, and the acceleration became coherent with both muscles at 7 Hz. During the 2.5 s cycle time, the acceleration record became coherent with both muscles at 3–4 Hz as well. In the most rapid jaw movements (1.25 s cycle time), the 7 Hz peak was still present, but the coherence shifted to the lower frequencies, including 0.8 and 2.4 Hz which are harmonics of the cycle frequency.

A similar general pattern is evident in subject B. In this example, there is weak coherence between both muscles and the peak tremor (around 6 Hz) when the mandible was in the rest position. The strength of the coherence increased during the slowest jaw movements and again during the 5 s cycle time movement. As in subject A, peaks at lower frequencies (0.4, 1.6 and 2.4 Hz for the 2.5 s cycle; 0.8, 2.4 and 4 Hz for the 1.25 s cycle) then became dominant in the acceleration spectrum, and these were coherent with the activity in both muscles.

This pattern of coherence of both muscles with the resting tremor frequency at 6–7 Hz, that shifted rather abruptly to coherence at around 2 Hz at the fastest cycle times was observed in most instances.

Finger tremor

Finger tremor in the 8–12 Hz range was minimal when the middle finger was held at rest in a neutral, near-horizontal position, and was evident in the acceleration spectra in only four out of eight subjects. The power spectra for finger and jaw movements in one subject at rest and during rhythmical movements at different cycle times are shown in Fig. 3. When the subject rhythmically flexed and extended the finger at increasing speeds, the amplitude of the spectral density at the peak tremor frequency increased significantly in all subjects (repeated measures ANOVA: $F = 9.21$, $P < 0.001$). However, in contrast with the mandible, the peak frequency of the finger spectra did not change with increasing movement velocity. Note that because of the larger range of possible movement of the finger, the maximal angular displacement of the fingertip during the voluntary movements was about 45 deg compared with about 30 deg for the jaw; hence, the finger accelerations resulted in higher angular velocities than in the jaw.

The mean peak tremor frequency in the accelerometer records from the finger was 8.4 ± 1.9 Hz, which was significantly higher than the 6.2 ± 1.2 Hz average peak frequency of resting jaw tremor in these subjects (Student's paired *t* test, $P = 0.019$, 9 degrees of freedom).

DISCUSSION

It is well established that the limbs tremble when held in various postures. This physiological tremor increases during stress and following strenuous exercise, and is often greater in the elderly (reviewed by Deuschl *et al.* 2001). It is less widely known that the mandible also trembles at a low frequency when held at or near its rest position (Palla & Ash, 1979; de Vries *et al.* 1984). However, its amplitude is usually too small to be detected by the naked eye.

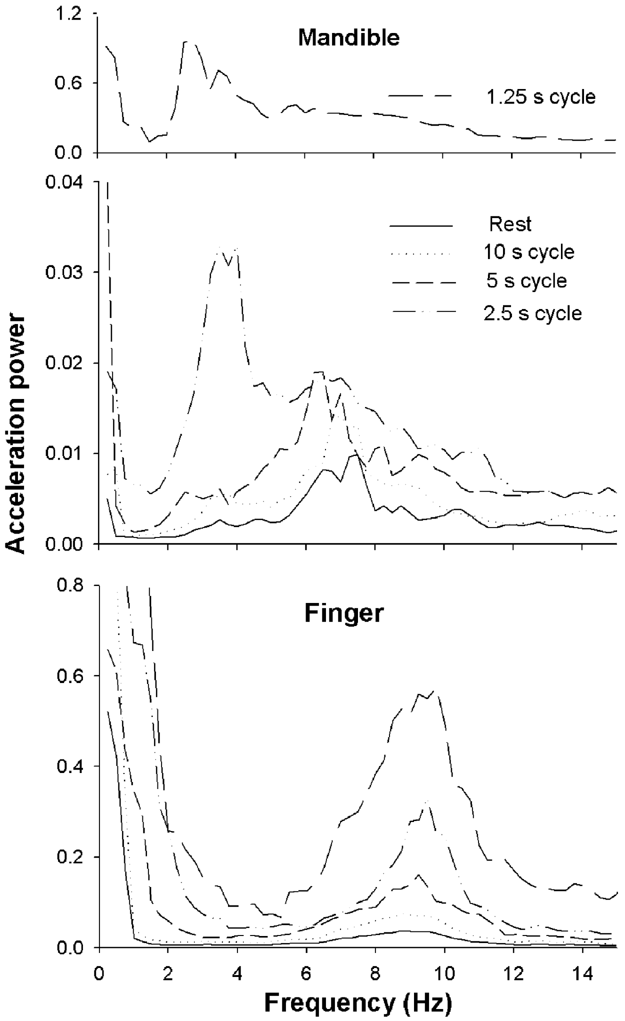

Figure 3. Comparison of power spectra from accelerometers on the mandible and finger

Power spectra from accelerometers on the mandible and on the middle finger of one subject at rest and during rhythmical jaw-opening and -closing movements and rhythmical finger flexion and extension, respectively, during tracking of a sawtooth target with cycle periods of 1.5, 2.5, 5 and 10 s. The upper and middle panels show the spectra obtained from the accelerometer on the mandible during various cycle times: note that the 1.25 s cycle time record is plotted at lower gain than the records in the middle panel. The lower panel shows the spectra for all finger movement cycle times. Note that because the range of jaw movement is smaller than the range of finger movement, the velocities of finger movements are greater than the velocities of jaw movements at corresponding cycle periods.

Jaw tremor has also been observed during weak isometric muscle contractions. Van Steenberghe & de Vries (1980) reported a very low-amplitude tremor ($< 10\ \mu$m) primarily in the range 3–8 Hz when the jaws were held with the edges of the incisor teeth just touching. (Note that this amplitude in itself is not very meaningful: when the teeth are in contact, their displacement is restricted to about this distance by the periodontal ligament in which they are suspended.) A similar tremor with an amplitude of about 0.6 mm and a mean power frequency near 7 Hz was recently observed in subjects biting gently against a spring-loaded position sensor with a force of about 0.08 N (Junge *et al.* 1998). The tremor was shown not to be a simple mechanical resonance because its frequency did not change when the mandible was loaded. Furthermore, the cardioballistic contribution to tremor was negligible at frequencies above the heart rate (about 1 Hz).

Junge *et al.* (1998) used a novel analysis to investigate the mechanisms underlying the tremor. While it is not possible to see very small periodic fluctuations in the raw surface EMG of the masticatory muscles when the jaw is in its rest position, coherence analysis is a powerful method for revealing any relationship between the EMG and the movement of the mandible in the frequency domain. Their demonstration of coherence between the centrally programmed modulation of masseter EMG and the jaw movement led to the conclusion that at least some of the 7 Hz resting tremor is due to rhythmical activation of the jaw-closing muscles.

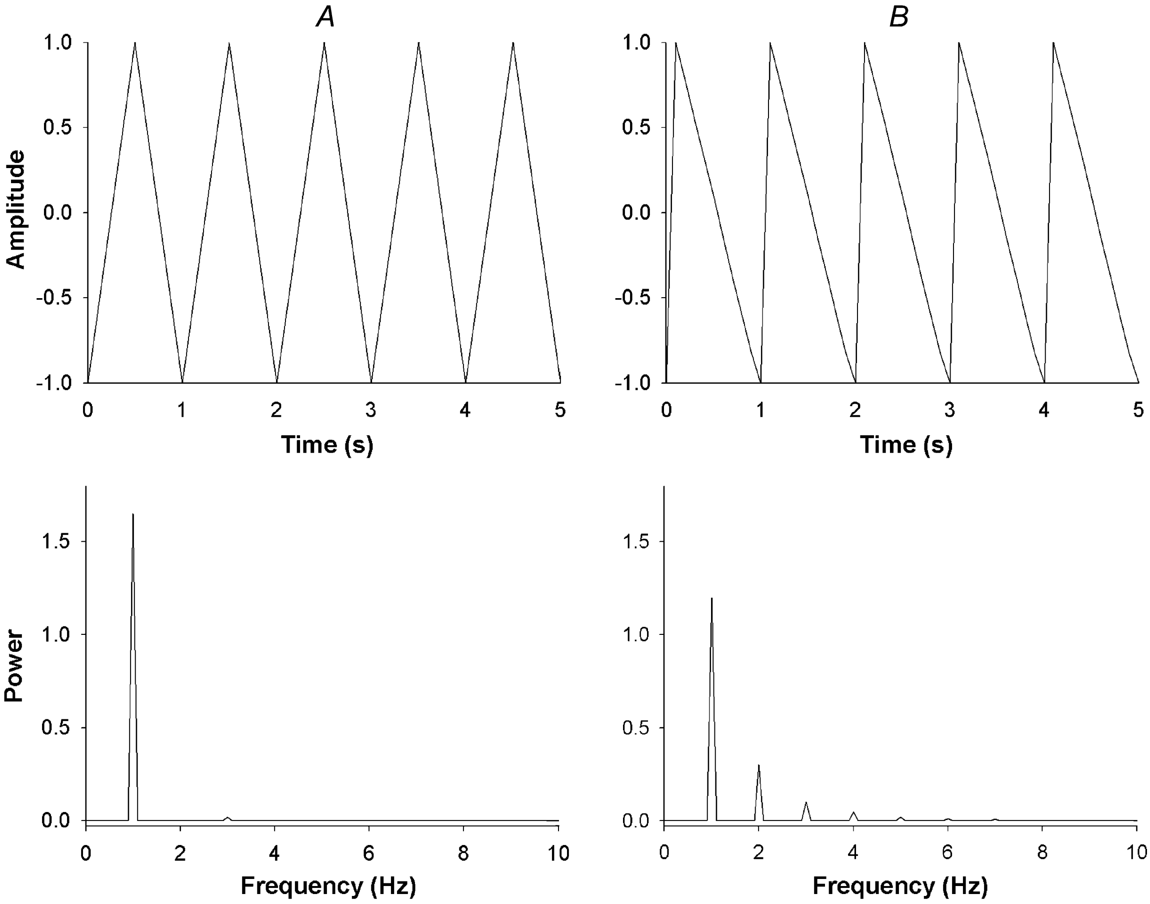

Figure 4. Spectral density of sawtooth waveforms

A, an artificially generated, symmetrical, sawtooth waveform similar to that used to drive the target line for the jaw and finger movements. (Note that the target line was projected on an oscilloscope screen with a high sweep speed giving the appearance of a horizontal line moving up and down at constant velocity). The waveform has a cycle time of 1 s, which equates to a frequency of 1 Hz. Its spectrum below is dominated by a narrow peak centred on 1 Hz. An asymmetrical waveform of the same amplitude and cycle time is shown in the upper panel of *B*. Its spectrum differs markedly from that of the symmetrical waveform in that the power in the primary 1 Hz peak is less, and secondary peaks appear at frequencies that are harmonics of the primary frequency. Hence, movements that accurately track a symmetrical sawtooth target waveform like those made by the finger will have a peak at the frequency of the target waveform, while movements that are intended to track a symmetrical target waveform but were in fact asymmetrical, will have not only a peak at the frequency of the target waveform but also subsidiary peaks at its harmonic frequencies.

However, this analysis did not reveal whether this neurogenic activity was reflex in origin, or the result of some other mechanism. Several authors have suggested that the mandible is maintained actively in its rest position partly by a stretch reflex that resists gravity (Møller, 1976; Goldberg & Derfler, 1977). In this scenario, short-latency stretch reflexes in the jaw-closing muscles would modulate their activity to maintain the rest position. The delays in the operation of the stretch reflex (Poliakov & Miles, 1994; Miles & Poliakov, 1997) would lead to small vertical movements of the mandible in a tremor-like pattern. Several observations argue against this possibility. Firstly, jaw closing is brought about by muscles with strong stretch reflexes, while jaw opening is produced primarily by the digastric muscles which have few, if any spindles (Dymtruk, 1974; Lennartsson, 1979) and lack normal stretch reflexes (see Luschei & Goldberg, 1981). Moreover, there are no crossed inhibitory stretch reflexes between the jaw-closing and -opening muscles (Kidokoro *et al.* 1968). Clearly, therefore, the alternating oscillatory activation of antagonistic jaw muscles cannot be the result of either switching between stretch reflexes in the jaw-opening and jaw-closing muscles, or crossed inhibitory stretch reflexes. The present demonstration that the antagonistic muscles are activated alternately (i.e. 150–180 deg out of phase) both at rest and during slow voluntary movements instead supports the idea that mandibular tremor is analogous to the pulsatile control that has been demonstrated in the finger muscles (Vallbo & Wessberg, 1993). In this model, a centrally located pulse generator sends alternating bursts of excitation to antagonistic muscle groups during slow voluntary movements. However, it should be noted that the low value of coherence in the tremor frequency in the resting mandible indicates that only a fraction of the tremor can be attributed to one masseter and one digastric muscle. Other influences, including activity in the other masticatory muscles from which we did not record, and the intrinsic mechanical resonance of the mandible may also be important.

This coherence between muscle activity and acceleration was observed in only half of the subjects while they sat with the jaw in the rest position, a proportion similar to that seen by Junge *et al.* (1998). However, coherence at the tremor frequency became evident in all subjects during slow, active jaw movements in which there was more muscle activity. That is, the coherence increased when the signal-to-noise ratio of the EMG was higher. This strongly suggests that the failure to demonstrate coherence at rest in some subjects is the result of the low signal-to-noise ratio of the surface EMG records of masseter and digastric muscles under this condition. It should also be noted that there are six separate jaw-closing muscles and four jaw-opening muscles; hence, the low values for coherence reported in this and the earlier study may indicate that phase-linked activity in the other muscles of mastication accounts for much of the tremor.

While the general concept of a pulsatile control mechanism fits the present observations, there are some differences between the pattern of pulsatile control of the masticatory muscles and of the finger. In particular, the pattern of spectra recorded from the mandible during active movements differs from that observed in the fingers, at least as the speed of movement increases. In both mandible and finger, the power at the tremor frequency increases with movement speed (cf. Figs 1 and 3). In the mandible, however, more rapid movements are also associated with the emergence of lower-frequency peaks. These are clearly the result of activity in the masticatory muscles, as they are highly coherent with masseter and digastric muscle activity (Fig. 1).

Since these peaks occur at harmonics of the cycle frequency, they point to distortion of the cyclical movement in the mandible; that is, the acceleration of the opening movements differed consistently from the acceleration of the closing movements. Figure 4 amplifies this point by showing the effect of asymmetry on the spectrum of a sawtooth signal. Figure 4*A* shows an artificially generated sawtooth with a 1 s cycle time, and its spectral density below. The spectrum has a sharp, narrow peak centred around 1 Hz, which is obviously the dominant frequency in the waveform. When the sawtooth is made asymmetrical in Fig. 4*B*, there is still a dominant 1 Hz peak (i.e. 1 s cycle time), but this is reduced in amplitude, and some of the power of the signal now appears at the harmonics of 1 Hz. Hence in Fig. 1, the low-frequency peaks in the acceleration spectra of the higher-velocity movements are a reflection of asymmetries in the acceleration of the mandible during opening and closing movements (despite the subjects' efforts to follow the symmetrical sawtooth target). In contrast, the spectra of the finger movements in the present (e.g. Fig. 3) and earlier studies show no such asymmetries, indicating that the finger movements remained smoothly cyclical at higher velocities, so that the tremor (pulsatile control) peak continued to dominate the spectra.

The other low-frequency peaks in the jaw and finger spectra can be explained in terms of the kinetics of the movement task. The high-amplitude peaks for coherence at 0.8 Hz in both subjects correspond with a low-amplitude peak in the spectrum of the movement (e.g. Fig. 1). The small peak in this jaw spectrum probably reflects the mean frequency of the jaw-opening and -closing movement (a cycle time of 1.25 s corresponds with a movement frequency of 0.8 Hz). That is, the coherence at this frequency is probably the result of the regular alternating activation of the masseter and digastric muscles at this frequency to produce the cyclical jaw movement. The absence of such peaks at frequencies corresponding to slower cycle times is probably due both to the very small accelerations during these cycles and to the very low frequency of the harmonics of such cycles (0.1, 0.2, 0.3, 0.4 for the 10 s cycle; 0.2, 0.4, 0.6, 0.8 for the 5 s cycle). In this very low frequency range, it is not possible to distinguish any harmonic peaks (cf. Fig. 3, middle panel).

It is concluded that the mandible has a low-amplitude tremor at rest, which is at a frequency below that of physiological tremor in the fingers. The tremor both in the rest position and during voluntary movements is not the result of a reflex-based position servo that maintains the resting jaw position, but is the consequence of centrally generated, alternating bursts of activity in the jaw-opening and jaw-closing muscles. The role of this low-frequency pulsatile activation of motoneurons in the control of jaw position at rest and during slow voluntary movements remains to be elucidated.

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