

## Reflex ‘unloading’ and ‘defensive capitulation’ responses in human neck muscle

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1. We studied unloading and stretch responses in human neck muscles during manoeuvres in which the head pulled against a 2–3 kg weight which could be abruptly released or applied electromagnetically.
2. During head tracking in pitch, unloading of the weight induced inhibition of EMG in the contracting sternocleidomastoid at a mean latency of 24.9 ms in normal subjects and at 41 ms in bilateral labyrinthine-defective subjects, with antagonist (trapezius) excitation at 30.5 and 41.3 ms, respectively. During tracking in yaw, unloading induced inhibition in the contracting splenius capitis (SpC) at a mean latency of 20.4 ms in normal subjects and 25 ms in labyrinthine-defective subjects, with excitation in the antagonist SpC at 22.2 and 24 ms, respectively.
3. If subjects tried to resist an unexpected sideways tug on the head a burst occurred in the stretched SpC at a mean latency of 53.5 ms. When subjects relaxed there was excitation of the shortening SpC at 75.9 ms, which assisted the imposed motion and is possibly a ‘defensive reflex’.

The study of motor control in neck muscle has, until recently, been concerned exclusively with the interaction of vestibular-colic and stretch-induced cervico-colic reflexes, whose respective functions are to stabilize the head in space and on the trunk. The latencies of these reflexes, their dynamic properties and behaviour under different tasks have been identified in both human (Bronstein, 1988; Gresty, 1989; Keshner & Peterson, 1995; Keshner, Cromwell & Peterson, 1995) and animal studies (Keshner, Baker, Banovetz & Peterson, 1992). However, recent experimental data (Kanaya, Gresty, Bronstein, Buckwell & Day, 1995), suggest that human neck muscle also has other modes of reflex motor control. These authors reported ‘unloading responses’ similar to those seen in other skeletal muscle (Angel, Eppler & Iannone, 1965; Prochazka & Dewhurst, 1970; Marsden, Merton & Morton, 1976; Traub, Rothwell & Marsden, 1980; Marsden, Rothwell & Day, 1983), which were observed in both normal and labyrinthine-defective

human subjects during abrupt tilt of the trunk from upright (Kanaya *et al.* 1995). For example, as the trunk tilted backwards, about a head-centred axis, the head initially remained relatively stable in space because of inertia, which meant that dorsal neck muscles were shortened. In these muscles burst activity was observed at latencies < 100 ms, whilst still shortened, with inhibition of the antagonist; a pattern of activity which maintained the upright posture of the head. This type of response in neck muscle is similar to that observed in the human thumb flexor (Marsden *et al.* 1976) when there is either a sudden release of the support surface, or the arm is withdrawn, whilst the subject attempts to maintain a constant contact pressure with his thumb.

The drawback of tilting the whole subject is that the stimulus is of slow, indeterminate onset and does not permit accurate determination of latency, and thereby, the organization of reflex pathways and location of the sensory transducers which trigger the responses. Here, we report

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simple techniques which we have used to expose the head to high acceleration perturbations. The results show for the first time that an unloading response can be evoked in human neck muscle reliably and at short, consistent, latencies. The studies have also revealed the existence of what may be a 'defensive reflex' response not previously observed in the neck.

## METHODS

### Subjects

In all ten normal subjects (age range, 22–49 years; 3 females, 7 males), and six subjects (age range, 35–73 years; 2 females, 4 males) with bilateral absence of labyrinthine function gave their informed consent to the studies according to the guidelines of the local ethics committee.

On clinical examination, all labyrinthine-defective subjects had saccadic ('broken up') compensatory eye movements and admitted oscillopsia (visual instability due to absent vestibulo-ocular reflex compensatory eye movement) in response to rapid head shaking in pitch and yaw. Nystagmus responses to 20 °C caloric irrigation were absent. Steps of 80 deg s<sup>-1</sup> in rotational velocity and peak velocity sinusoidal rotation in yaw at frequencies up to 1 Hz failed to provoke nystagmus in the dark. Three labyrinthine-defective subjects tested for vestibulo-myogenic responses in the neck to high intensity click stimulation (Colebatch & Halmagyi, 1992; Colebatch & Rothwell, 1993) had absent responses.

### Unloading during neck flexion–extension (pitch)

Ten normal subjects and four labyrinthine-defective subjects performed this experiment. Each sat upright, with the trunk restrained but the head free to move, and viewed a cathode ray tube (CRT) which was centred at eye-level and at a distance of 40 cm, and which presented a horizontal target line. The line moved vertically at a constant speed up and down the screen through a distance of 10 cm peak to peak at 0.2 Hz repetition frequency. The subject wore a tightly fitting, elasticated, head band on which was mounted an electromagnetic six-dimensional displacement transducer (Polhemus Fastrack®; Polhemus Kaiser Aerospace Electronics Co., VT, USA) and a linear piezo-resistive accelerometer with its sensitive axis aligned sagittally. The pitch-rotation signal from the Fastrack was displayed as a second horizontal line on the CRT.

Attached to the headband at the occiput was an inelastic string which looped over a pulley (Fig. 1) so that the head supported and lifted a 3 kg weight (2 kg for women). The weight could be detached from the string by an aerial bomb electromagnetic catch which opened in < 1 ms, thus unloading the head.

EMG activity was recorded using MSB Unilect™ Ag–AgCl, solid state, surface electrodes (MSB Ltd, Wiltshire, UK) mounted over the belly of the sternocleidomastoid (SCM) muscles and over the upper trapezius muscles. The signals were amplified and analog filtered with a passband of 32 Hz to 3.2 kHz. The task of the subject was to track the target line on the CRT, attempting to superimpose the pitch displacement line from the Fastrack, by moving his head in pitch synchronously with the stimulus.

The peak-to-peak head rotation compensating for peak-to-peak target displacement was 35 deg.

On random cycles during downwards head rotation (neck flexion) when the weight was being raised, the catch was released just after the head had passed through the primary position so that the

anterior muscles were contracted and the subject attempted to resume accurate tracking as soon as possible.

All signals were acquired at 1 kHz sampling rate for A/D conversion and an average of rectified responses to ten weight releases was obtained for each subject. Ten cycles of weight lifting without release were acquired for comparison.

### Unloading during horizontal neck rotation (yaw)

Ten normal subjects and four labyrinthine-defective subjects performed this experiment. Each subject sat with the trunk restrained and head tracking as before (see above), but with the target and tracking lines oriented vertically on the screen and moving horizontally. The linear piezo-resistive accelerometer was oriented with its sensitive axis aligned with the tangent to yaw rotation.

The string was attached to a small flat rectangle of hard rubber which was held between the front teeth. The string exited from the left side of the mouth horizontally in the frontal plane so that it pulled tangentially to the arc of rotation. The string then looped over a pulley (Fig. 1) and suspended a 2 kg weight out of sight of the subject. As the head rotated from left to right through 50 deg peak to peak the weight was lifted.

On random cycles during rightwards head rotation, when the weight was being raised, the catch was released mid-cycle detaching the weight, as above, and the subject attempted to resume tracking. Signals were acquired and averages of ten responses were made as above.

### Abrupt loading in the yaw plane

Seven normal subjects performed this experiment. Ten responses were obtained for averaging in each of the conditions.

**Active resisting.** The subject sat motionless, with head and eyes in their primary positions viewing the vertical target line. The string was held in the mouth, as for Yaw unloading, but it exited from the right side of the mouth and did not bear weight. The 2 kg weight was still attached to the subject via the bite, but was suspended by a second string which was held in the catch. After random intervals the catch was released causing the weight to fall momentarily before taking up the slack on the string held in the subject's teeth. The duration of the fall estimated from the catch release to the onset of head acceleration ranged from 12–22 ms, delivering estimated impulsive momenta of 0.236–0.432 kg m s<sup>-1</sup>. The falling weight jerked the head to the right whilst the subject's task was to keep his tracking line aligned on the CRT with the target line.

**Passive motion.** The subject was instructed to relax and not to oppose the weight. When the weight was allowed to fall freely it hit the ground after inducing approximately 40 deg of head rotation.

EMG for all yaw rotation studies was obtained from splenius capitis (SpC), and masseter muscles. The electrodes were located over SpC by placement 2 cm from the mid-line and 2 cm below the external occipital eminence. This is a position from which no EMG activity is recorded during voluntary shoulder elevation which would involve trapezius muscle (Mazzini & Schieppati, 1994).

## RESULTS

### Pitch unloading

In normal subjects, abrupt unloading during the weight-lifting phase of head movement, when the head was moving forwards and downwards, produced a stereotyped movement: the head suddenly moved in advance of the

target for *circa* 300 ms then slowed down to resume target trajectory at > 700 ms (Fig. 2A b, position trace).

The unloading caused an instantaneous spike of head acceleration (peak tangential linear acceleration of the forehead varied from 0.2 to 0.5 g) from which latency measurements were made on EMG responses. EMG activity in the contracting unloaded muscle (i.e. SCM) showed an inhibitory period (Fig. 2A b, EMG traces) at a mean latency of  $24.9 \pm 2.5$  ms ( $\pm$  s.d.), followed by a burst of excitation at a mean latency of  $73.1 \pm 6.7$  ms. The antagonist trapezius muscle showed an excitatory burst at  $30.5 \pm 5.4$  ms.

Labyrinthine-defective subjects had a similar pattern of response but with slightly delayed latencies (Fig. 2B b: their mean latency for inhibition in the unloaded muscle was  $41 \pm 6$  ms with later excitation at  $95.3 \pm 11$  ms. The burst of activity in their trapezius had a mean latency of  $41.3 \pm 5.9$  ms. The control traces (Fig. 2A a and B a) demonstrate that the SCM is predominantly involved in weight lifting during this phase of tracking, with relative quiescence of the trapezius.

Mann-Whitney *U* tests showed significant differences between normal subjects' and labyrinthine-defective subjects' latencies for inhibition in SCM ( $P < 0.01$ ), excitation in SCM and excitation in trapezius ( $P < 0.05$ ).

**Unloading during yaw**

Unloading during yaw head rotation also produced stereotyped responses. As for pitch, the head moved ahead of the target abruptly when the weight was released and after *circa* 300 ms made a return to target trajectory which was attained at about 700 ms (Fig. 3, position traces). A

similar spike of tangential acceleration attaining 0.4–0.6 g peak signalled the release of the weight with no effective time delay (Fig. 3).

In normal subjects the EMG in the contracting unloaded muscle (right SpC) showed an inhibitory period (Fig. 3A b, EMG trace) at a mean latency of  $20.4 \pm 3.6$  ms, followed by a burst of excitation at a mean latency of  $55.9 \pm 12.5$  ms. The antagonist, left SpC showed an excitatory burst at  $22.2 \pm 7.9$  ms.

All of the four labyrinthine-defective subjects (2 of these were studied in pitch) had responses which appeared normal (Fig. 3B b): their mean latency for inhibition in the unloaded (right) muscle was  $25.0 \pm 3.1$  ms with later excitation at  $70.0 \pm 8.5$  ms. The burst of activity in the antagonistic (left) SpC had a mean latency of  $24.0 \pm 4.4$  ms.

The control traces (Fig. 3A a and B a) demonstrate that the right SpC is predominantly involved in weight lifting during this phase of tracking with relative quiescence of its antagonist.

Mann-Whitney *U* tests showed no significant differences between normal subjects' and labyrinthine-defective subjects' latencies.

A period of inhibition of on-going activity was also observed in masseter muscle at similar latencies of  $9.8 \pm 1.7$  and  $11.3 \pm 2.1$  ms in normal subjects and labyrinthine-defective subjects, respectively.

**Abrupt loading in yaw plane**

The effect of sudden loading was to rotate the head from its primary position to the right, stretching the left SpC with

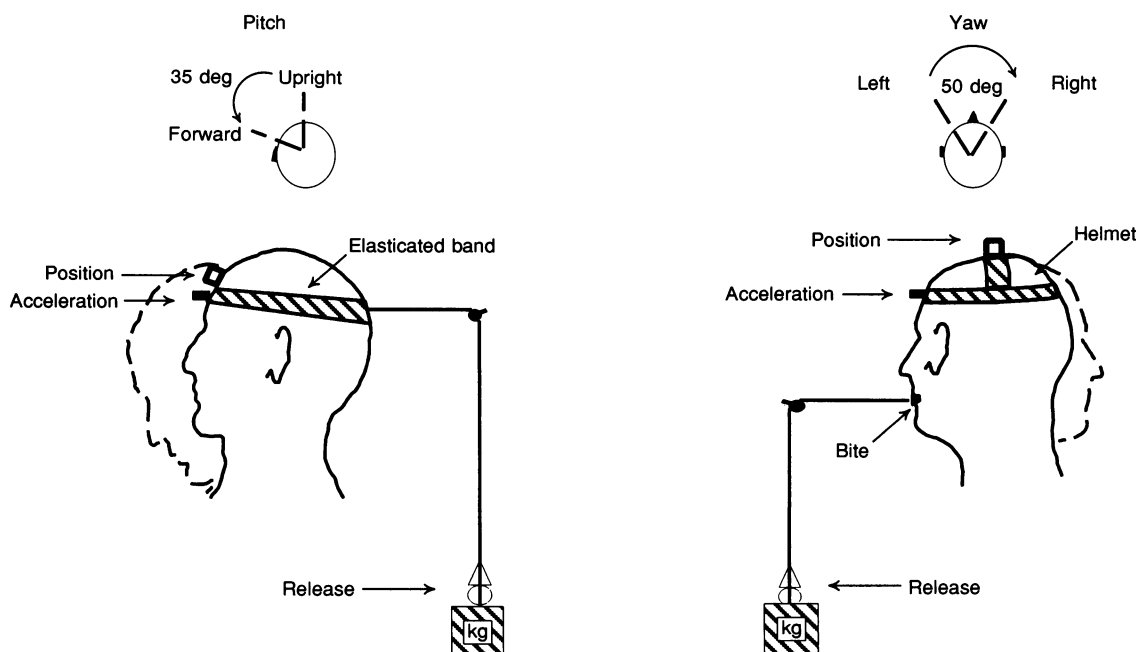


Figure 1. Apparatus for subjecting the head to abrupt unloading

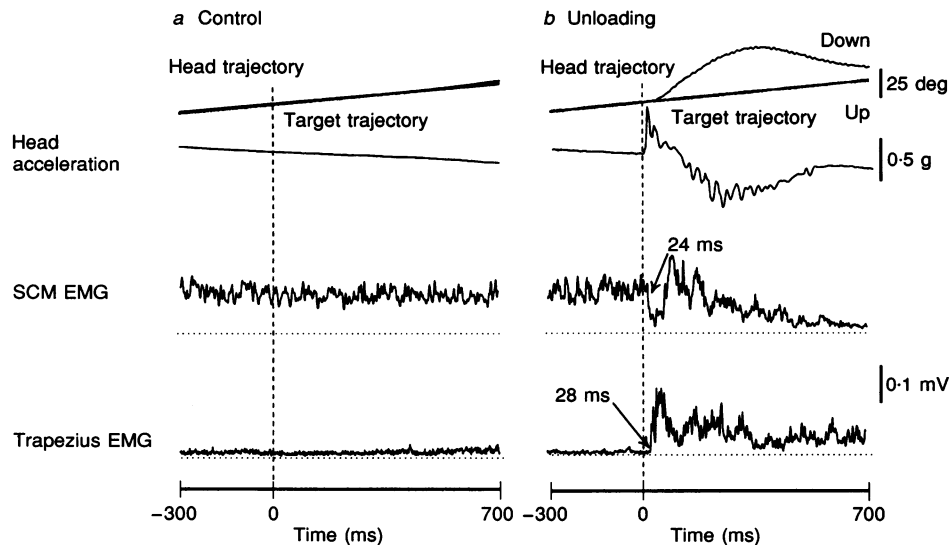
relative contraction of the right SpC. The loading caused an instantaneous sharp onset of acceleration from which latencies could be measured (Fig. 4A).

When *actively resisting* against sudden loading, subjects regained their primary position after about 500–700 ms, their heads having been displaced typically by < 10 deg

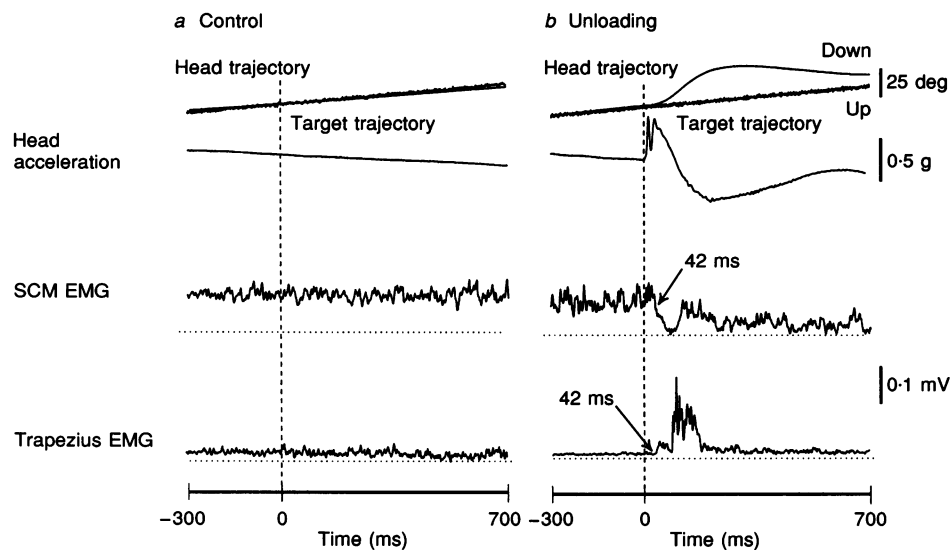
(Fig. 4Aa). A burst of activity was observed at a mean latency of  $53.5 \pm 7.3$  ms in the stretched muscle. The right SpC was silent until > 100 ms (Fig. 4Aa).

The masseter muscle also showed a period of inhibition at a latency of  $8.3 \pm 1.9$  ms as it did with the yaw rotation (Fig. 4Bb).

### A Normal subject



### B Labyrinthine-defective subject



**Figure 2.** Unloading responses in neck muscle during pitch movements

*Aa* and *Ba*, control levels of rectified EMG in the sternocleidomastoid (SCM) and trapezius muscles during head movement without unloading. *Ab* and *Bb*, responses to unloading in these muscles. *A*, results from a normal subject; *B*, results from a labyrinthine-defective subject. The trajectory of the head movement is shown overlaid upon the visual target trajectory. Each trace shows an average of 10 trials. In this and subsequent figures, the vertical dashed lines show the start of head acceleration. The horizontal dotted lines in the EMG traces in this figure and in Fig. 3 indicate the zero level of EMG voltage.

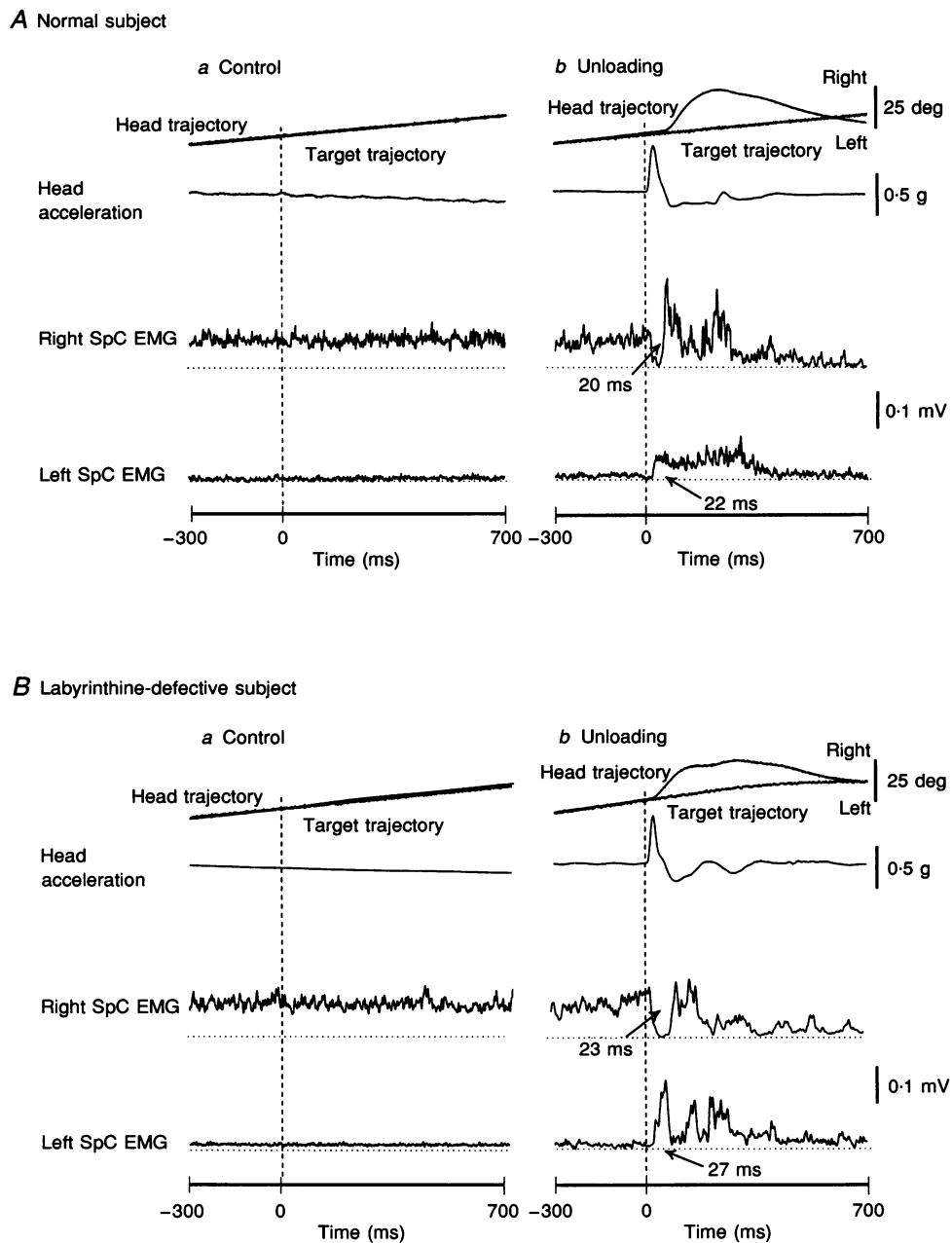
When *passive*, the subjects' heads were pulled rightwards by the falling weight until it hit the floor. The overall head rotation induced was *circa* 40 deg.

There was an inversion of the pattern of EMG observed when the subjects were active, with an excitatory burst in the right SpC, i.e. the shortened muscle, at a mean latency of  $75.9 \pm 5.0$  ms. This burst would have assisted the rotation of the head. The stretched left SpC showed a minimal excitation at the same latency (Fig. 4*A b*) in some subjects,

whilst in others there was no activity in the stretched muscle.

### DISCUSSION

General considerations which apply to interpreting all experimental results are that the stimuli deployed gave tactile, dental and, in some subjects, perhaps faint auditory signals about the time of onset of head accelerations. It is unlikely that these inputs, which were similar across

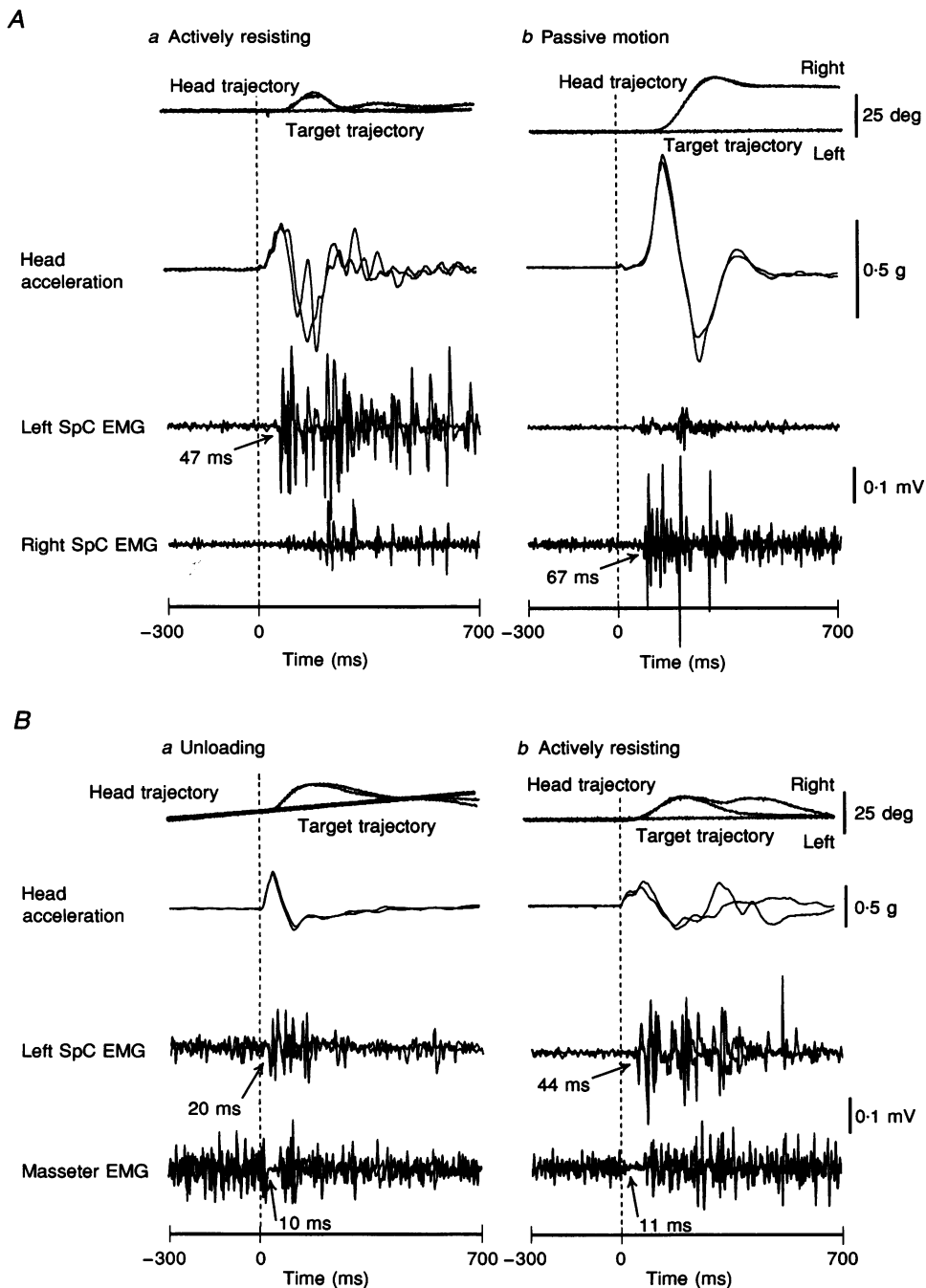


**Figure 3. Unloading responses in neck muscle during yaw movements**

*Aa* and *Ba*, control levels of EMG in the left and right splenius capitis (SpC) muscles during head movement without unloading. *Ab* and *Bb*, responses to unloading in these muscles. *A*, results from a normal subject; *B*, results from a labyrinthine-defective subject. The head trajectory is overlaid on the visual target trajectory. Each trace shows an average of 10 trials.

conditions and groups of subjects, are responsible for the variable patterns of the responses observed, but they may have had a facilitatory effect. The latencies of responses observed were all well below the minimum latencies established for voluntary head movement responses (Mazzini

& Schieppati, 1992). Subjects were not 'gambling' on the timing of the stimuli since the response latencies observed were similar across subjects, had small variance and none coincided with, or preceded, the stimuli.



**Figure 4.** Comparison of responses in neck muscle during loading and unloading

*A*, responses (overlay of 2 trials of the same experiment) in neck muscle (splenius capitis; SpC) when the head was exposed to a tug in yaw from the falling weight: *Aa*, 'Actively resisting', the subject was instructed to resist the tug; *Ab*, 'Passive motion', the subject was instructed to relax. *B*, a comparison (overlay of 2 trials of the same experiment) of the shorter latency of activation of SpC when unloaded during yaw motion (*Ba*) with the longer latency response when the muscle is stretched by a tug in yaw (*Bb*). By way of contrast the control traces of activity in masseter show that the stimuli evoke trigeminal responses at constant latency.

### Unloading responses

We have demonstrated that abrupt unloading of human neck muscle during active contraction causes a short latency, marked inhibition of the contracting muscle and an almost synchronous sudden burst of the antagonist. For yaw, the latencies of these activities are uniquely short: the burst in the antagonist muscle at 22 ms is half that found for the stretch reflex in the same muscle (54 ms) evoked when the muscle was at a comparable length. Other studies also report long latencies for stretch reflexes in the neck; 51 ms (Horak, Schupert, Dietz & Horstmann, 1994) and 60 ms (Ito, Corna, von Brevern, Bronstein, Rothwell & Gresty, 1995). These latencies are much longer than those of stretch reflexes in limbs, probably because it is difficult to stretch neck muscle quickly. Therefore, on the basis of latency and pattern, which is organized to compensate for the sudden release of weight, the response to unloading is probably a distinct 'unloading' reflex.

The origin of the unloading response could be in the sudden shortening of the spindles in the load-bearing muscle, which occurs during the voluntary contraction when the weight is released. The sudden change in signals from the spindle and/or tendon organ may give the ipsilateral inhibition together with contralateral excitation through a crossed pathway.

In normal subjects the 'unloading' response may have a vestibular component, which would be an appropriate response to the head perturbation at a conveniently short latency. However, in labyrinthine-defective subjects the response is probably more purely myotactic, with similar properties to the unloading reflex demonstrated for the thumb (Angel *et al.* 1965; Prochazka & Dewhurst, 1970; Marsden *et al.* 1976). The similarity to reflexes in the thumb may imply that there is  $\alpha\gamma$ -coactivation in neck muscle during voluntary head movement.

In normal subjects, for pitch, when vestibular-colic and unloading responses would be co-directional, the possibility is open that the earlier part of the response beginning at *circa* 20 ms is primarily vestibular. In labyrinthine-defective subjects the response can be seen uncontaminated by vestibular-colic responses evoked by the sudden head jerk and hence, occurs at a slightly longer latency of 40 ms. Therefore, in normal subjects, the myotactic component of the whole unloading response may come in at a later stage, after the vestibular component.

### Unloading response latency

In labyrinthine-defective subjects, the latency of the unloading response in SpC at *circa* 20 ms for yaw was approximately half that in SCM for pitch. This is comparable to the difference in latencies for the respective stretch reflexes in these muscles. The latency of the stretch reflex in SpC is 40 ms, as shown by the 'active stabilization' protocol, whereas the latency in SCM is 60 ms (Ito *et al.*

1995). There is no difference in latencies between SpC and SCM response following cortical (Berardelli, Priori, Inghilleri, Cruccu, Mercuri & Manfredi, 1991) or vestibular (click-evoked; Di Lazzaro, Quartarone, Higuchi & Rothwell, 1995) activation, so the delay of reflexes in SCM may be attributable either to differences in reflex loop times of cranial and cervical muscle, on which there is no evidence, or alternatively, it may arise from differences in the mechanical action of these muscles. It is possible that a rotational displacement of the head in yaw gives an immediate stretch to SpC, whereas pitch rotation from the primary position may not because of the complex geometry of neck extension. In pitch, the head may translate backwards or forwards as well as rotate. Translation would probably not stretch the SCM immediately. Thus, the relative proportion of translation to rotation could delay the stretch in SCM.

Since the subjects were biting to retain head loading it could have been possible that the responses seen in neck muscle were mediated by trigeminal stimulation. However, there are reasons for rejecting this hypothesis. Although response latencies in SpC were quite different during active stabilization, which produced a stretch reflex, as opposed to unloading (44 and 20 ms, respectively), the latency in masseter remained at a constant 10 ms (Fig. 4Ba). In addition the mental branch of the trigeminal nerve does not appear to have a strong projection to the neck (Di Lazzaro *et al.* 1995).

### 'Capitulatory response'

Electrical stimulation of the infra-orbital branches of the trigeminal nerve (Di Lazzaro *et al.* 1995) in human subjects evokes an excitatory response in contralateral SpC at a latency of 11.8 ms; presumed to be a 'defensive withdrawal' response parallel with the effects of stimulation of vibrissae in animals (Abrahams, Kori, Loeb, Richmond, Rose & Keirstead, 1993). We have found the inverse of this type of response in that a sudden tug on the teeth in a relaxed subject activates muscle which assists the head in following the direction of the imposed force, i.e. 'going with the tug'. Synchronous with the capitulatory burst is evidence for a suppressed stretch reflex in the antagonist muscle (Fig. 4A b, compare left SpC responses).

The current studies and recent papers (Ito *et al.* 1995; Kanaya *et al.* 1995) present a set of techniques which have shown that human neck muscle supports the variety of automatic responses that have been demonstrated for the hand (Marsden *et al.* 1976; Traub *et al.* 1980; Marsden *et al.* 1983). Presetting of the functional organization of the spinal motor neurone pool for neck muscle by task clearly determines an appropriate pattern of response to test stimuli. Hitherto, this richness in modes of automatic control has been neglected in studies of human head movement.

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