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## Postural Muscle Tone in the Body Axis of Healthy Humans

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**Gurfinkel, Victor, Timothy W. Cacciatore, Paul Cordo, Fay Horak, John Nutt, and Rachel Skoss.** Postural muscle tone in the body axis of healthy humans. *J Neurophysiol* 96: 2678–2687, 2006. First published July 12, 2006; doi:10.1152/jn.00406.2006. Across the entire human body, postural tone might play its most critical role in the body's axis because the axis joins the four limbs and head into a single functioning unit during complex motor tasks as well as in static postures. Although postural tone is commonly viewed as low-level, tonic motor activity, we hypothesized that postural tone is both tonically and dynamically regulated in the human axis even during quiet stance. Our results describe the vertical distribution of postural muscle tone in the neck, trunk, and hips of standing human adults. Each subject stood blindfolded on a platform that axially rotated the neck, trunk, or pelvis at 1°/s and  $\pm 10^\circ$  relative to the neutral position (i.e., facing forward). The measured resistance to axial rotation was highest in the trunk and lowest in the neck and was characterized by several nonlinear features including short-range stiffness and hysteresis. In half of the subjects, axial muscle activity was relatively constant during axial rotation, and in the other half, muscle activity was modulated by lengthening and shortening reactions, i.e., decreasing activity in lengthening muscles and increasing activity in shortening muscles, respectively. Axial resistance to rotation was reduced in subjects whose muscle activity was modulated. The results indicate that axial tone is modulated sensitively and dynamically, this control originates, at least in part, from tonic lengthening and shortening reactions, and a similar type of control appears to exist for postural tone in the proximal muscles of the arm.

### INTRODUCTION

The study of muscle tone has a long history, principally due to its clinical value, as most movement disorders are accompanied by a change in muscular tone. Historically, the clinical characterization of altered muscle tone has been a valuable aid to diagnosis, even though the mechanisms contributing to muscle tone remain poorly understood.

Muscle tone is usually described as the resistance of a limb to passive movement (Foster 1892), where the resistance arises from passive and involuntary active forces. Measuring the resistance of the limbs is straightforward because appendicular muscles are oriented along the skeletal axes, and joint rotation causes roughly proportional changes in muscle length. Consequently, most of what is known about muscular tone in humans has been derived from studies of the limbs.

The axial and proximal muscles comprise a significant part of the human skeletal musculature and differ from those of the limbs in terms of anatomical structure, innervation, and function. Therefore it is important to understand how muscle tone is distributed and controlled among the proximal and axial

muscles because postural tone might also differ between the appendicular and axial muscles.

The axial musculature is architecturally complex. Axial muscles have broad anatomical origins with insertions linked to several structures—the spine, pelvis, rib cage, and shoulder girdle. Many of the axial muscles span long distances and have multiple attachments to multiple bones. The muscle fascicles in most axial muscles are oriented at different angles to the longitudinal axis of the spine (Kiefer et al. 1998), forming, with the spine, a structure reminiscent of a vertical antenna with lateral guy-wires.

The descending control of axial muscles originates from a wide variety of cortical and sub-cortical structures. The somatic descending brain stem pathways provide an important source of control to the axial muscles, including the interstitial tract, tectospinal tract, lateral and medial vestibulospinal tracts, reticulospinal tract from the pontine, medullary and mesencephalic medial tegmental fields, and fibers from the nucleus of the posterior commissure (Kuypers 1964, 1981). The innervation of spinal interneurons and motoneurons by these pathways is both uni- and bilateral (Holstege 1996). The monoaminergic descending systems also regulate muscle tone, including serotonergic fibers from the raphe nuclei, noradrenergic fibers from the locus coeruleus, the subcoeruleus, and the medial and lateral parabrachialis nuclei, and a small contingent of dopaminergic fibers. The descending fiber tracts of these monoaminergic modulatory pathways influence specifically the tonic firing patterns of spinal motoneurons (Hounsgard et al. 1988; Hultborn 1999). A third structure, the limbic system, also influences postural tone (Holstege 1998).

Because the axis links all parts of the body together, axial tonic activity from these diverse descending structures must take into account the actions of all parts of the body during the maintenance of posture and during movement. During movement of one part of the body, other parts of the body are disturbed, creating disequilibrium. Thus the precise movement of distal segments can be realized only by stabilizing more proximal segments (Hasan 2005; Hess 1943). Such combinations of stability and mobility in everyday motor activities depend on the precise regulation of axial and proximal tonic activity. Despite the biomechanical importance of the axial muscles to posture and movement and, as a consequence, the importance of the tonic regulation of these muscles, almost nothing is known about the distribution and regulation of axial tone.

The classical studies of muscle tone were carried out early in the 20th century using decerebrate and spinally transected

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animal models (Magnus 1924; Sherrington 1898, 1909, 1915). These early studies characterized muscle tone as muscle activity that is long-lasting and fatigue resistant, susceptible to interruption from reflex inhibition, sensitive to changes in head position (termed tonic neck and vestibular reflexes), and plastic, by virtue of “lengthening” and “shortening” reactions. In this case, plasticity refers to the ability of a joint to assume different positions without a change in tonic muscle tension. The lengthening reaction involves a *decrease* in muscle activity during muscle *lengthening*, and the shortening reaction involves an *increase* in muscle activity during muscle *shortening* (Sherrington 1909), that is, opposite in sign to the stretch reflex.

Considering the variety of functions and complex innervation of axial and proximal muscles, axial tone might also have unique characteristics. Therefore the experiment described in this paper was designed to characterize axial tone, its distribution, and its adaptation to different postures. We hypothesized that in healthy humans, changes in the lengths of axial and proximal muscles as a result of changes in posture can result in shortening and lengthening reactions. These reactions might endow the axial and proximal musculature with the property of plasticity (i.e., change in length with no change in tension), which could be useful in stabilizing the head, trunk, and pelvis. To investigate this hypothesis, we constructed a device to quantify tone in standing human subjects at different levels of the axis. We employed very slow, torsional rotation to efficiently lengthen and shorten the obliquely oriented neck, abdominal, and back muscles, while not displacing the body center of gravity or restricting standing posture in any direction other than torsionally. We then compared axial tone to that of the proximal arm muscles under conditions of involuntary tonic tension to determine whether muscle tone is controlled similarly in different parts of the body. The results of this study were previously described in abstract form (Cacciatore et al. 2004).

## METHODS

A total of 22 active human subjects (ages 24–65), including 11 females and 11 males without histories of spinal injury or back pain, provided informed consent according to procedures mandated by the Oregon Health & Sciences University Institutional Review Board. Each subject stood blindfolded on a horizontal platform that rotated slowly about a vertical axis roughly congruent with the subject's spinal column. The resistance of the subject's body to torsional motion was measured at different levels of the body axis, while electromyographic (EMG) signals were recorded from the muscles of the trunk. To test for reproducibility of results, three subjects were tested twice, and six subjects were tested three times, always with a 1-mo separation between experimental sessions. The possibility of voluntary interference in torsional resistance to rotation was excluded by requiring four subjects to perform mental calculation (i.e., counting backward from 100 by threes) while their neck torque was measured.

### Measurement of axial tone

Each subject stood on a rotating platform enclosed by a rigid, steel frame, as shown in Fig. 1A. Torsional strain was applied to the neck, trunk, or pelvis in an alternating right- and leftward pattern at a velocity of  $1^\circ/\text{s}$ . The angular distance of rotation was  $\pm 10^\circ$  relative to the body midline, making the duration of a full cycle 40 s. Under these conditions, the blindfolded subjects had only a vague sense of the

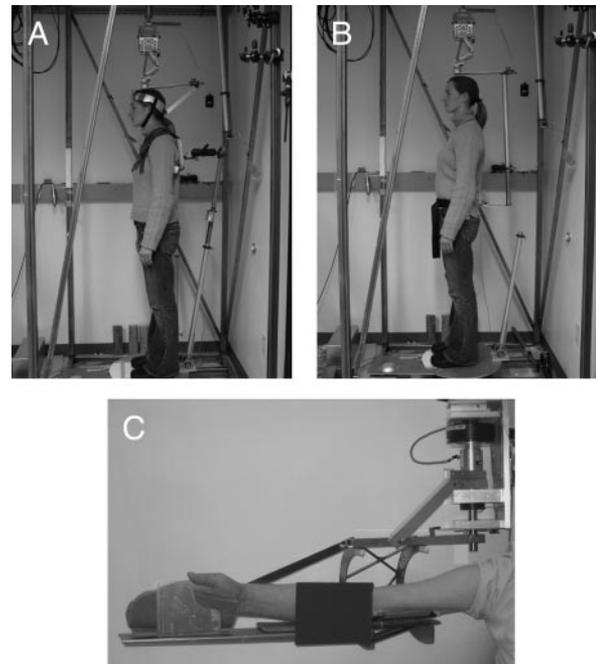


FIG. 1. Tone measurement apparatus. The device for measuring axial tone is shown in A and B and that for measuring shoulder tone is shown in C.

motion of the body. Torsional motion was isolated to a particular level of the axis by two rigid rods. One rod was hinged at one end to the rotating platform and attached with a harness to the pelvis or shoulders (i.e., Fig. 1A). As torsional motion was applied to the axis, we measured the torsional resistance to rotation with a load cell mounted to a suspension system via a second rigid rod. Depending on the level of desired rotation, this second rod was attached either to the head via a helmet or to the shoulders or pelvis via a harness. The setup in Fig. 1A was used to measure the axial resistance to trunk rotation. The suspension system for measuring axial torque restricted motion only in the torsional direction, while allowing free movement of the subject, over a limited range, in all other directions. The stiffness of the suspension system was  $590 \text{ Nm}^\circ$  in the torsional direction, but only  $0.25 \text{ N/cm}$  for translation in the  $x$ ,  $y$ , and  $z$  directions. The weight of the suspension device was counterbalanced by a coil spring. Similarly, the rod delivering motion from the rotating platform allowed unrestricted anterior-posterior and lateral sway. An angular displacement transducer provided a signal corresponding to platform position. Torque and platform rotation were digitized and recorded at 50 Hz.

### Measurement of muscle tone in the shoulder

A separate device was used to rotate the right shoulder to compare tone in the arm to that in the axis to determine whether postural tone was controlled similarly in biomechanically complex and simple systems. As shown in Fig. 1B, the shoulder device consisted of an arm support, a servo-controlled motor, a gear box, a clutch, a torque sensor, and an optical potentiometer to measure the shoulder angle. The axis of rotation of the device was collinear with the axis of rotation of the shoulder. Releasing the clutch allowed the subject free horizontal movement at the shoulder, and engaging the clutch allowed the motor to rotate passively the shoulder in the horizontal plane. During shoulder rotation ( $1^\circ/\text{s}$ ,  $\pm 10^\circ$ ), we recorded the EMG activity of the right anterior deltoid and right pectoralis major.

In the standing human, tone is elevated to maintain the standing posture against gravitational force. To place the arm in a heightened state of tonic activity comparable to quiet standing, we employed the Kohnstamm phenomenon (Kohnstamm 1915)—the development of

involuntary muscle contraction and movement following sustained voluntary contraction. The postcontraction Kohnstamm state was induced with the subject's right arm in the shoulder device, the clutch disengaged, and weights attached to the device via a cable and pulley system. First, the subject's maximum voluntary contraction (MVC) level was determined for horizontal flexion of the arm at the shoulder. Then, after a 1- to 2-min rest period, the subject lifted 25% of the MVC weight and held it stationary for a period of 15–20 s, at which point the weights were removed and the subject relaxed the arm. After 1–2 s, EMG activity appeared in the shoulder flexors and built up in amplitude (e.g., Fig. 7B, top trace).

On inducing the postcontraction state, two testing procedures were then carried out. In the procedure performed first, which was designed to measure the duration of the postcontraction state, the clutch was maintained in the disengaged state, and an involuntary, slow horizontal flexion of the shoulder was observed (e.g., Fig. 7B, bottom trace). After a period of 10–15 s, EMG activity began to decrease, and after an additional 15–25 s, the shoulder movement stopped. In the second procedure, after the induction of the postcontraction and a stable level of shoulder flexor EMG, the clutch was engaged, and the shoulder was passively rotated in the horizontal plane. During some shoulder rotations, the shoulder was passively flexed, paused, and then extended to the original position, and then it was extended, paused, and then flexed to the original position. During other shoulder rotations, the order was reversed with respect to direction (see Table 3).

#### Measurement of EMG activity

We measured EMG activity in 12 subjects using bipolar surface Ag-AgCl electrodes placed over the muscle bellies in parallel with the muscle fibers. EMG activity was recorded bilaterally from external oblique, multifidus, and the medial and lateral heads of longissimus in 12 subjects and, in addition, the sternocleidomastoidus and splenius muscles of the neck in 8 subjects. The reference electrode was located over the clavicle. The raw EMG signal was amplified (1,000 times) and digitized (2,000 samples/s) without further modification.

Off-line, the EMG activity was band-pass filtered (50–500 Hz) and full-wave rectified. We defined the depth of EMG modulation during axial rotation as the difference between the maximum and minimum in EMG activity, as a percentage of the amplitude of background activity (e.g., Fig. 6). To distinguish between muscles in which EMG was or was not modulated by axial rotation and, if so, to determine the angular threshold for modulation, the threshold for modulation was defined as the angular displacement at which the modulation exceeded 3 SD of the baseline activity.

#### Data analysis

Significant differences in torque magnitude across subjects or across the vertical levels of axial rotation (i.e., pelvis, trunk, neck) were tested using a one-way ANOVA with  $\alpha = 0.05$ . Correlations between variables were described by Pearson's correlation coefficient and the overall significance of the regression.

## RESULTS

#### Mechanical response to axial rotation

The resistance of the neck, trunk, and pelvis to axial rotation ( $\pm 10^\circ$ ;  $1^\circ/\text{s}$ ) are illustrated in Fig. 2A for a representative subject. By convention, upward movement of the position record corresponds to leftward rotation of the feet, and upward movement of the torque records corresponds to the rightward-directed torque resulting from leftward rotation. As shown for the subject whose data are depicted Fig. 2A, axial resistance to torsional motion was highest in the trunk (3 Nm), intermediate in the hips (1 Nm), and lowest in the neck (0.2 Nm). Requiring subjects to perform mental arithmetic during axial rotation produced no detectable change in the torque recordings.

On average ( $n = 22$ ),  $\pm 10^\circ$  axial rotation resulted in a peak-to-peak torque resistance of  $0.5 \pm 0.2$  Nm to neck rotation,  $5.1 \pm 1.9$  Nm to trunk rotation, and  $3.2 \pm 1.7$  Nm to hip rotation (see Table 1). An ANOVA showed a significant effect of the level (i.e., neck, trunk, and pelvic) on the peak-to-peak amplitude of axial torque [ $F(2,56) = 37.6$ ;  $P < 0.001$ ]. At each level, there was a large variation in peak-to-peak torque across subjects, but relatively little variation within subjects (e.g., Fig. 2B). In subjects tested at least twice, a paired  $t$ -test showed no significant difference between the test-retest measurements of peak-to-peak amplitude of trunk torque ( $t = 0.31$ ,  $P = 0.76$ ,  $n = 9$ ). On average, the peak-to-peak torque magnitude was significantly lower in women than in men—in the neck, by 46.4% [ $F(1,20) = 5.0$ ;  $P < 0.05$ ]; in the trunk, by 28.5% [ $F(1,20) = 20.6$ ;  $P < 0.005$ ]; and in the pelvis, by 46.0% [ $F(1,13) = 10.5$ ;  $P < 0.01$ ]. Within each gender group, there was no apparent correlation between axial resistance to twisting and body mass or other anthropometric measure.

The detailed torque responses to axial rotation contained a number of nonlinear properties, some of which indicate

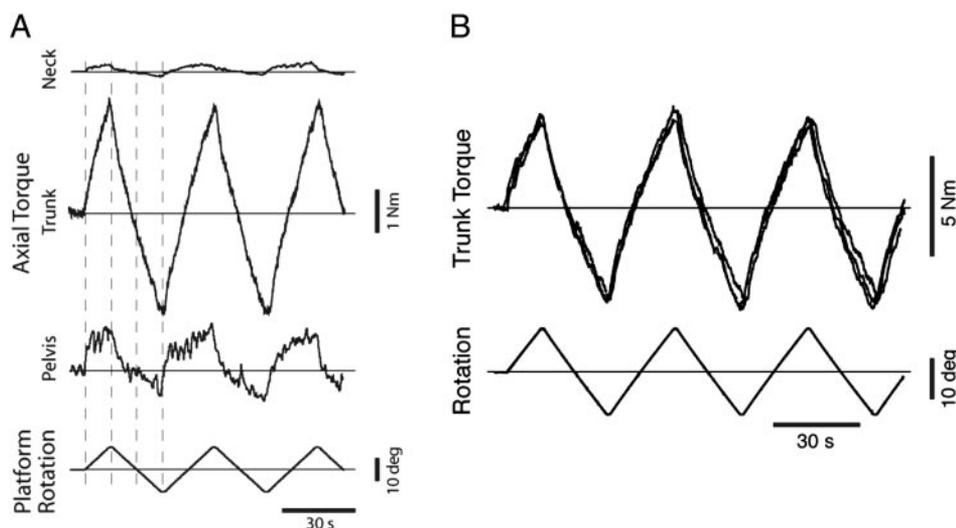


FIG. 2. Torque responses of the neck, trunk, and pelvis to axial rotation. *A*: same scaling is applied to all 3 levels of the axis. Periodic fluctuations in trunk and pelvis torque records correspond to the breathing pattern. *B*: 3 trunk torque records are superimposed from 3 experimental sessions with the same subject, held at 1-mo intervals.

TABLE 1. Peak-to-peak torque magnitude (Nm)

| Gender                    | Trunk       | Hip         | Neck        | Hip/Trunk   | Neck/Trunk  |
|---------------------------|-------------|-------------|-------------|-------------|-------------|
| M                         | 8.69        | 4.80        | 0.88        | 0.55        | 0.10        |
| M                         | 7.62        | 6.78        | 0.82        | 0.89        | 0.11        |
| M                         | 7.56        | 4.38        |             | 0.58        |             |
| M                         | 6.63        | 3.69        | 0.82        | 0.56        | 0.12        |
| M                         | 6.61        | 4.72        |             | 0.71        |             |
| M                         | 6.50        | 4.37        | 0.69        | 0.67        | 0.11        |
| M                         | 6.43        | 4.47        | 0.63        | 0.70        | 0.10        |
| M                         | 4.53        | 2.17        | 0.37        | 0.48        | 0.08        |
| M                         | 4.31        | 2.65        | 0.70        | 0.61        | 0.16        |
| M                         | 3.51        | 2.40        |             | 0.68        |             |
| M                         | 3.10        | 5.77        | 0.58        | 1.86        | 0.19        |
| Average (Male)            | 5.95 ± 1.82 | 4.20 ± 1.41 | 0.69 ± 0.16 | 0.75 ± 0.38 | 0.12 ± 0.04 |
| F                         | 7.09        | 4.18        | 0.70        | 0.59        | 0.10        |
| F                         | 6.99        | 3.98        |             | 0.57        |             |
| F                         | 5.46        | 1.00        | 0.26        | 0.18        | 0.19        |
| F                         | 5.34        | 4.78        | 0.66        | 0.89        | 0.12        |
| F                         | 4.20        | 1.88        | 0.21        | 0.45        | 0.05        |
| F                         | 3.89        | 2.07        | 0.22        | 0.53        | 0.06        |
| F                         | 3.55        | 1.41        | 0.27        | 0.40        | 0.08        |
| F                         | 2.83        | 1.48        |             | 0.52        |             |
| F                         | 2.65        | 1.22        |             | 0.46        |             |
| F                         | 2.48        | 1.40        | 0.27        | 0.57        | 0.11        |
| F                         | 2.38        | 1.52        |             | 0.64        |             |
| Average (Female)          | 4.26 ± 1.73 | 2.27 ± 1.36 | 0.37 ± 0.21 | 0.53 ± 0.17 | 0.10 ± 0.05 |
| Average (Male and Female) | 5.11 ± 1.94 | 3.23 ± 1.67 | 0.54 ± 0.24 | 0.64 ± 0.31 | 0.11 ± 0.04 |

Values are means ± SD.

the influence of active contraction on the torque responses. As shown for one subject in Fig. 3A, the first 1–2 s after the onset of trunk rotation resulted in a steep rise in the trunk torque, after which torque increased more slowly (\*). In the first cycle of rotational motion, the first 2° of torsional rotation typically increased axial torque twice that during the corresponding phase in the second cycle. This nonlinearity in the torque response of the axial muscles is similar to short-range stiffness previously described during stretch of individual muscle fibers or whole muscle in resting and

active states (e.g., Flintney and Hirst 1978; Rack and Westbury 1974).

A second, commonly observed nonlinearity was a phase-advance of axial torque with respect to the angular position of the axis. After the onset of platform rotation, each time the platform passed through the neutral position (--- in Fig. 3A), axial torque had already passed through zero (· · ·), which indicates that the neutral position had shifted toward the direction of rotation. This shift could result from a combination of active and passive properties.

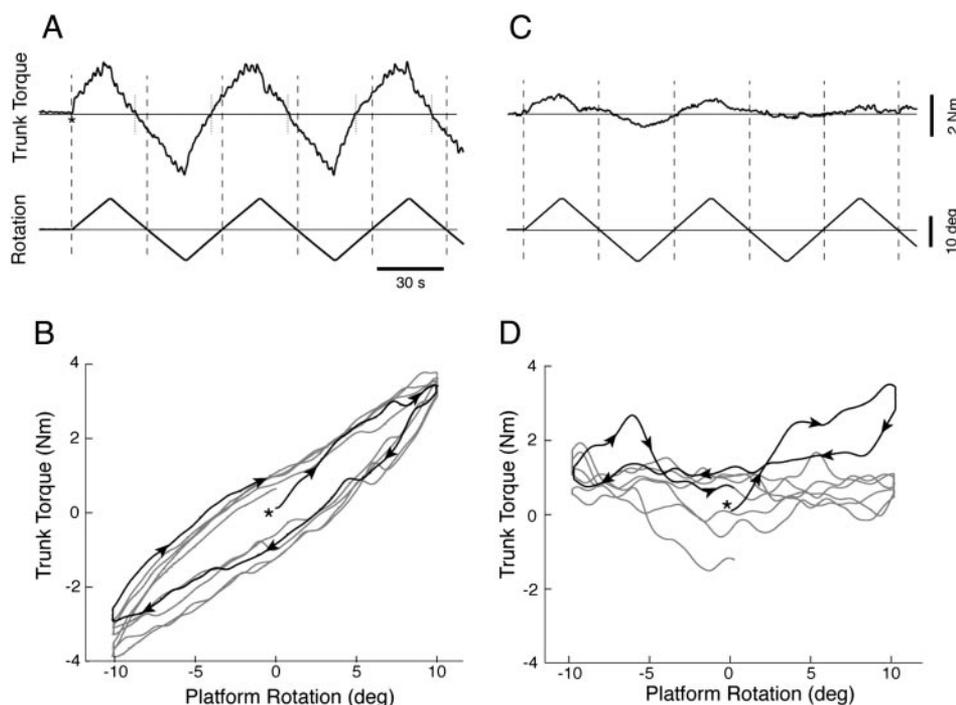


FIG. 3. Nonlinear properties of axial resistance. A and C: trunk torque is shown for 2 different subjects. A: \*, onset of short-range stiffness; ---, phase-advance of torque. B and D: relationship between trunk torque and platform rotation is shown for the same 2 subjects; \*, onset of short-range stiffness. The subject whose data are shown in A and B was relatively stiff and lacked modulated electromyography (EMG) in the axial muscles. The subject whose data are shown in C and D was relatively flexible and had modulated EMG in the axial muscles. Torque position and time calibrations are the same in A and C.

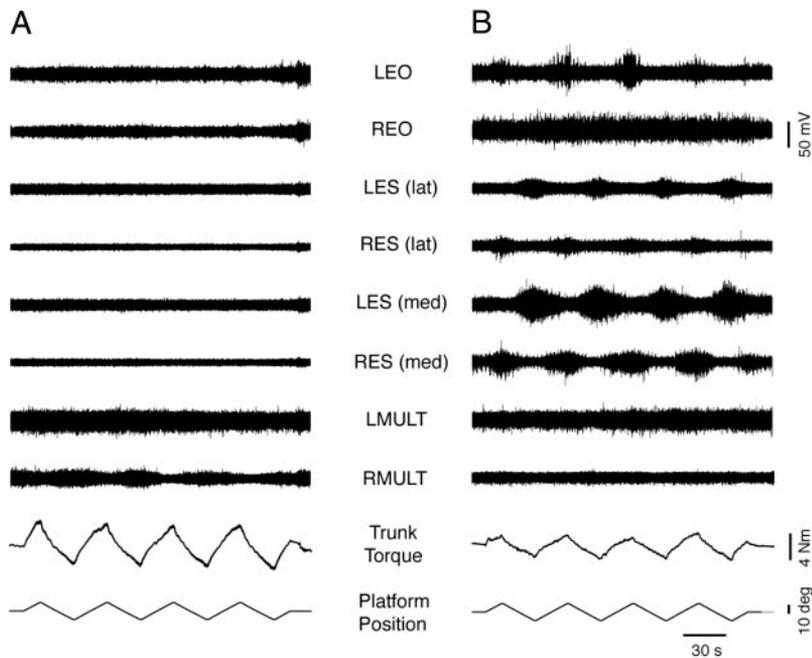


FIG. 4. Unmodulated and modulated EMG responses to axial trunk rotation. Recordings of EMG during trunk rotation are shown for 2 representative subjects, in *A*, whose EMG was unmodulated, and in *B*, whose EMG was modulated. LEO, left external oblique; REO, right external oblique; LES(lat), left lateral head of erector spinae; RES(lat), right lateral head of erector spinae; LES(med), left medial head of erector spinae; RES(med), right medial head of erector spinae; LMULT, left multifidus; RMULT, right multifidus.

Short-range stiffness and phase advance resulted in hysteresis between axial torque and axial position, as shown in Fig. 3 for trunk rotation in two subjects exhibiting qualitatively different behavior. The subject whose axial torque is shown in Fig. 3, *A* and *B*, was relatively stiff and showed little modulation of EMG (e.g., Fig. 4*A*). The phase advance described in Fig. 3*A* is evident in Fig. 3*B* as a positive torque as the platform passes through the neutral position in subsequent cycles. Approximately half of the subjects showed a stable relationship between angle and torque, as exemplified in Fig. 3, *A* and *B*. In contrast, the subject whose axial torque is shown in Fig. 3, *C* and *D*, was relatively flexible and showed clear modulation of EMG (e.g., Fig. 4*B*). In these more flexible subjects, the torque-angle relationship was more variable and had a lower slope (Fig. 3, *C* and *D*). A low slope of the torque-angle relationship indicates relatively little resistance to axial rotation, which can be explained by a change in the level of axial muscle activity. Variability in the torque-angle relation was observed more commonly in the hip and neck than in the trunk.

To quantify the variability in the torque-angle relationship, we measured the SD of the peak-to-peak torque. The SD in peak-to-peak magnitude was inversely correlated with magni-

tude of torque modulation ( $R^2 = 0.61$ ,  $P < 0.001$ ), inferring that, in these subjects at least, active processes are involved in controlling muscle activity in response to changes in length.

#### Muscle activity in response to axial rotation

All neck and trunk muscles from which we recorded exhibited background EMG activity during 15 s of quiet standing, prior to the initiation of platform rotation (Fig. 4). This background activity was tonic with low-amplitude, between 20 and 30  $\mu$ V in all muscles including those on the ventral and dorsal neck and trunk.

In half of the subjects ( $n = 11$ ), muscle activity remained at background levels during axial trunk rotation with only a small, irregular modulation, as illustrated for one subject in Fig. 4*A*. Thus shortening and lengthening of the axial muscles did not change the level of tonic EMG activity. The other half of the subjects ( $n = 11$ ) exhibited a recurring modulation of EMG activity, phase-locked to platform rotation, as illustrated by one subject in Fig. 4*B*. In the latter subjects, EMG modulation had a synergistic pattern between muscles in opposite quadrants of the axis (e.g., ventral-right vs. dorsal-left) and a

TABLE 2. Depth of EMG modulation of trunk muscles

| Subject | Amplitude, Nm | ES(l)            | ES(m)            | MLT             | EO              |
|---------|---------------|------------------|------------------|-----------------|-----------------|
| 1       | 2.0           | 2.8 $\pm$ 1.4    | 7.3 $\pm$ 2.9    | 10.1 $\pm$ 4.8  | 44.3 $\pm$ 16.3 |
| 2       | 2.7           | 4.9 $\pm$ 2.1    | 1.9 $\pm$ 1.9    | 5.0 $\pm$ 3.3   | 27.7 $\pm$ 15.9 |
| 3       | 2.8           | 73.5 $\pm$ 33.1  | 30.9 $\pm$ 10.6  | 31.7 $\pm$ 10.1 | 52.5 $\pm$ 17.2 |
| 4       | 3.5           | 21.4 $\pm$ 7.5   | 6.0 $\pm$ 2.5    | 18.6 $\pm$ 4.9  | 40.2 $\pm$ 15.8 |
| 5       | 3.9           | 116.7 $\pm$ 16.2 | 144.7 $\pm$ 23.5 | 16.9 $\pm$ 8.2  | 33.3 $\pm$ 15.7 |
| 6       | 6.6           | 15.6 $\pm$ 7.2   | 11.2 $\pm$ 10.2  | 30.5 $\pm$ 24.8 | 11.4 $\pm$ 9.7  |
| 7       | 6.8           | 20.8 $\pm$ 9.3   | 24.9 $\pm$ 9.8   | 23.5 $\pm$ 10.2 | 3.4 $\pm$ 4.4   |
| 8       | 6.9           | 1.8 $\pm$ 1.1    | 1.4 $\pm$ 1.4    | 12.8 $\pm$ 5.9  | 14.6 $\pm$ 7.9  |
| 9       | 7.0           | 12.4 $\pm$ 5.1   | 11.8 $\pm$ 3.8   | 27.6 $\pm$ 7.1  | 18.6 $\pm$ 10.6 |
| 10      | 7.5           | 73.2 $\pm$ 27.9  | 15.5 $\pm$ 9.8   | 31.4 $\pm$ 35.4 | 11.5 $\pm$ 24.6 |
| 11      | 7.6           | 10.5 $\pm$ 6.0   | 9.2 $\pm$ 6.0    | 28.2 $\pm$ 12.1 | 13.1 $\pm$ 8.4  |
| Average |               | 32.1 $\pm$ 38.0  | 24.1 $\pm$ 41.0  | 21.5 $\pm$ 9.4  | 22.5 $\pm$ 19.1 |

EMG, electromyograph; ES, erector spinae; MLT, multifidus; EO, external oblique.

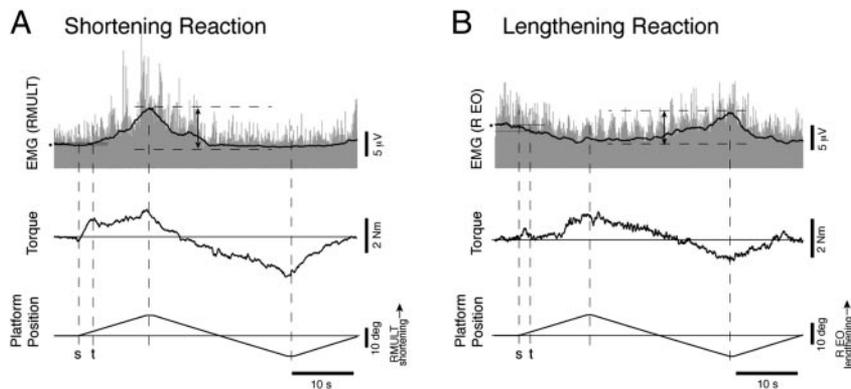


FIG. 5. Lengthening and shortening reactions in the trunk muscles. Muscle activity is shown for 2 cycles of trunk rotation, in *A*, for the right multifidus, and in *B*, for the right external oblique. Note the anti-phase nature of EMG and muscle length. The dark line in the EMG record represents the smoothed EMG signal, and the horizontal dashed lines demarcate the local maxima and minima in EMG amplitude.

reciprocal action in adjacent quadrants (e.g., ventral-right vs. ventral-left). Modulation of activity in two or more muscles across all cycles of axial rotation was defined as “modulatory.” Average depth of modulation ranged between 1.4 and 144.7% of baseline activity, depending on the subject (see Table 2). The single-cycle examples provided from one subject in Fig. 5 indicate a depth of EMG modulation of ~150% for a shortening reaction and 120% for a lengthening reaction. Table 2 provides values of average modulation depth for each muscle and each subject. While the modulatory pattern and depth varied widely across the 11 subjects, pattern and depth were highly consistent within each subject.

Overall, the patterns of EMG modulation were consistent with lengthening and shortening reactions. Three specific patterns of EMG modulation were observed: increased EMG amplitude during muscle shortening ( $n = 10$ ), decreased EMG amplitude during muscle lengthening ( $n = 3$ ), and a combination of 1 and 2 ( $n = 3$ ) as shown for one subject in Fig. 5. The particular distribution of EMG modulation across muscles was specific to each subject, but in all subjects of a given category, it occurred within a majority of the muscles from which we recorded.

The threshold change in muscle length for eliciting these modulatory patterns of EMG was quite small. Muscle activity exceeded baseline levels during shortening, on average, at  $3.5 \pm 1.3^\circ$  of platform rotation. Muscles exhibiting a decrease in EMG activity during lengthening had a threshold of  $5.1 \pm 1.9^\circ$ . Lengthening reactions typically had a higher threshold and lower depth of modulation than shortening reactions. Thresholds for EMG modulation were converted from degrees of rotation to percent of resting muscle length on the basis of the morphometric data. McGill and Hoodless (1990) calculated

that the lengths of most trunk muscles change by  $<1\%$  during  $0\text{--}30^\circ$  axial rotation, suggesting that the threshold change in length for the observed shortening and lengthening reactions was  $\sim 0.1\text{--}0.2\%$  of resting muscle length.

Linear regression was used to analyze the relationship between the amplitude of EMG modulation and the peak-to-peak torque during axial rotation. The results of this analysis are presented in Fig. 6 for trunk torque and external oblique—the prime mover of the trunk in the torsional direction. The depth of external oblique modulation was inversely correlated with the magnitude of trunk torque, accounting for 75% of the large variation in magnitude across subjects ( $R^2 = 0.75$ ,  $P \leq 0.001$ ). This inverse relationship is consistent with the observed phasing of EMG activity (e.g., Fig. 4), and suggests the active modulation of axial torque in response to tonic or slow changes in muscle length.

To determine the extent that the phase advance reflected active changes in muscle tone, we examined the correlation between the depth of EMG modulation in external oblique and the phase advance of trunk torque relative to axial rotation (see Fig. 6*B*). The relationship showed a positive and significant correlation ( $R^2 = 0.54$ ,  $P \leq 0.01$ ).

#### Muscle activity in response to arm rotation

As with axial rotation, arm rotation was associated with lengthening and shortening reactions, but only in the postcontraction state when the level of tone was slightly enhanced relative to the resting state. With the arm in a relaxed state, shoulder rotation at  $1^\circ/\text{s}$  over  $\pm 10^\circ$  did not evoke any change in EMG activity in shoulder muscles (Fig. 7*A*). After 15 s of moderate voluntary contraction of the anterior deltoid and

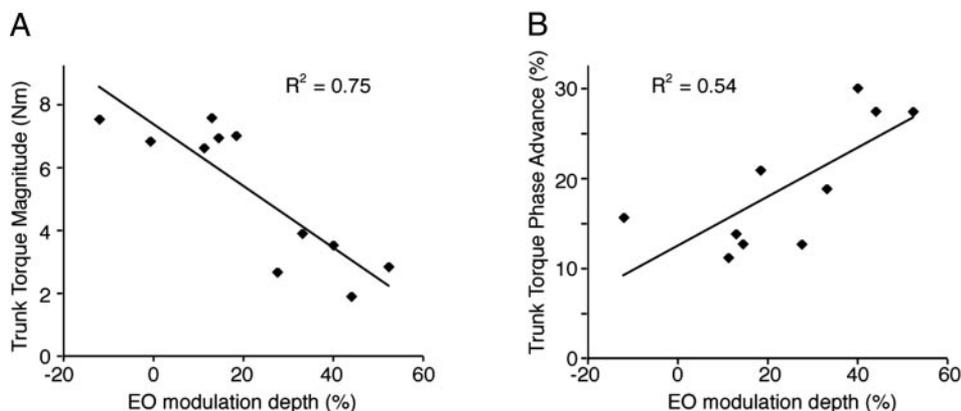


FIG. 6. Relation between external oblique and torque magnitude and phase advance. In *A*, peak-to-peak torque magnitude is inversely related to peak-to-peak external oblique EMG magnitude in 11 subjects (i.e., those with modulated EMG patterns). In *B*, the phase advance of trunk torque is positively correlated with peak-to-peak external oblique EMG magnitude in the same 11 subjects.

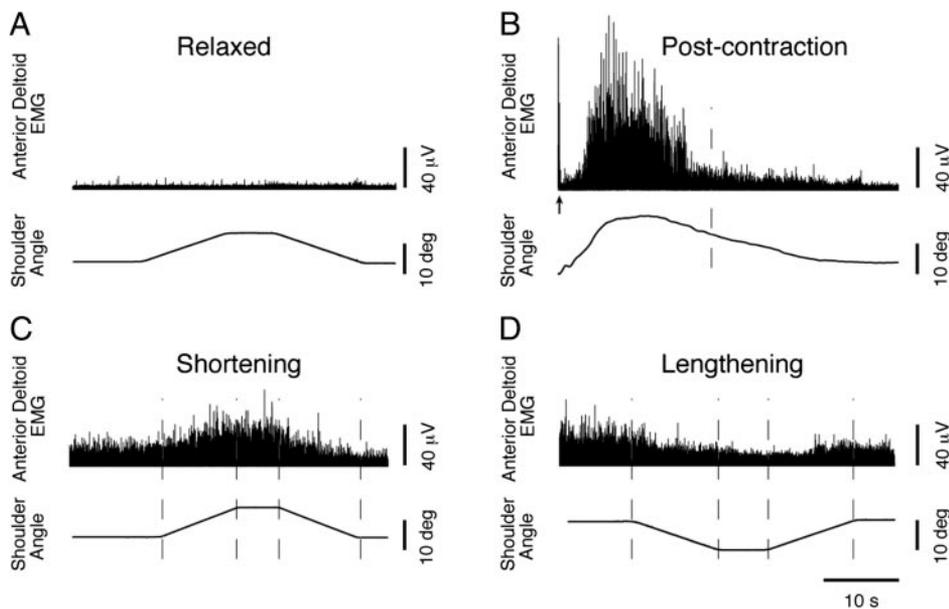


FIG. 7. Lengthening and shortening reactions in the shoulder muscles. *A*: shoulder muscles are relaxed and the shoulder is flexed and then extended at  $1^\circ/\text{s}$ . *B*: shoulder muscles become active and the shoulder rotates in the postcontraction state. *C*: after postcontraction activity and movement have declined (e.g., - - - in *B*), the shoulder is passively flexed evoking a shortening reaction. *D*: after postcontraction activity and movement have declined, the shoulder is passively extended evoking a lengthening reaction.

pectoralis major muscles, there was postcontraction activity in these muscles with a concomitant involuntary flexion of the arm for 30–40 s followed a return movement, which typically fell short the initial position (Fig. 7*B*). In a separate trial, the shoulder was passively rotated during the postcontraction state by engaging the clutch and driving the arm position at the time indicated by the dashed line in Fig. 7*B*. In the postcontraction state, shoulder rotation altered the EMG activity for both lengthening and shortening of the muscle. In all subjects who exhibited a postcontraction effect ( $n = 9$ ), muscle shortening resulted in increased EMG activity (e.g., Fig. 7*C*) and muscle lengthening resulted in decreased EMG activity (Fig. 7*D*). Shortening reactions of the tonically active shoulder muscles resulted in an average increase in EMG amplitude of 60.5%. Conversely, lengthening reactions resulted in an average decrease in EMG amplitude of 41.8%. In 13 of 17 trials (9 subjects), in which the passive shoulder rotation was reversed after a 5-s pause without reestablishing the postcontraction state, the sign of the reaction changed correspondingly; however, the amplitude of the second reaction was always less than that of the first.

## DISCUSSION

This study presents segmental torque and EMG activity to characterize, in standing subjects, the tonic postural activity of the axial and proximal muscles and the reactions of these muscles to changes in length during very slow, small axial rotations. The amplitude of the axial rotations imposed on the subject was limited to the neutral zones of the neck and thoraco-lumbar regions of the spine, where the musculoskeletal apparatus is relatively flexible and lax (Kumar 2004; Kumar and Panjabi 1995; Panjabi 1992). We propose therefore that most of the resistance to axial rotation was a product active muscle stretch. Nevertheless, it is possible that axial rotation evoked some resistive torque from noncontractile structures such as ligaments, capsular tissues of the joints, and muscle fascia. The first issue discussed is, therefore, the extent to which resistance to axial rotation is due to muscular moments

versus moments originating from passive structures. The second issue discussed is the relationship between axial torque and muscle force to understand how muscle tone differs at different axial levels. The third issue discussed is the nature of shortening and lengthening reactions and the role of these reactions in the regulation of postural tone.

### Source of resistive torque to axial rotation

The axial torque with which the trunk resisted rotation was twice that of the hips, and ten times that of the neck (Table 1). The relatively high resistance of the trunk and the relative complexity of the trunk musculoskeletal system suggest the possibility that the measured trunk torque reflects not only active muscular force but also passive nonmuscular forces from the joint capsules, ligaments, and fascia. The following observations suggest that resistive torque is primarily a product of active muscle force.

The nonlinear torque response to the linear motion employed in this study suggests the action of active muscle force. During the first cycle of axial rotation, the initial rate of rise of resistive torque was roughly twice that during the latter part of the cycle (e.g., Fig. 2), characteristic of short-range stiffness, which is most prominent in active muscle. In contrast, osteo-ligamentous structures of the spine characteristically resist linear stretch with an accelerating rise in force (Gal 1993).

Previous studies describing the EMG activity of trunk muscles during active voluntary rotation of the trunk (Kumar et al. 1996; Swie and Sakamoto 2004; Toren 2001) provide additional support for active muscular contributions to resistive torque during passive rotation. During voluntary trunk rotation of  $\leq 20$ – $30^\circ$ , the amplitude of muscle activity is quite small, but beyond  $20$ – $30^\circ$ , activity increases rapidly, presumably due to passive resistance from nonmuscular structures. The amplitude of axial rotation used in the present study (i.e.,  $\pm 10^\circ$ ) was two to three times smaller than the threshold for passive torsional resistance. The trunk has a neutral zone of at least  $\pm 10^\circ$  relative to the midline and can only be stabilized in this region by active muscle contraction (Kumar 2004; Kumar and

Panjabi 1995). In the present study, we showed a strong correlation of EMG activity with peak trunk torque, accounting for 75% of the variance across subjects (Fig. 6A). This high correlation between EMG activity and torque suggests that the measured trunk torque reflects active muscle contraction.

In the hips and neck, as well, active muscle tension probably contributes most of the resistance to axial rotation. The hips are synovial joints with extremely low friction, and their ligaments do not restrict movements unless the range of motion exceeds normal physiological limits. Therefore the hip ligaments are unlikely to deform significantly for the  $\pm 10^\circ$  of internal and external rotation used in the present study (e.g., Vharas et al. 1990). When the neck is rotated by  $\pm 10^\circ$ , torsional motion is restricted to the C<sub>1</sub>–C<sub>2</sub> segments, which have a relatively broad physiological range of motion of  $\pm 32$ – $60^\circ$  (Takahiro et al. 2004). The C<sub>1</sub>–C<sub>2</sub> joint is synovial and has a large neutral zone (Ishii et al. 2004; McClure et al. 1998; Panjabi 1992), which is much larger than the magnitude of the  $\pm 10^\circ$  rotation imposed in the present study.

Significant modulations from one cycle to the next in peak-to-peak muscle torque, peak-to-peak EMG amplitude (reciprocal to torque changes), and slope of the torque-angle hysteresis loop are all difficult to explain by the passive mechanical resistance of tissues. The moment arms of torsional trunk muscles are an order of magnitude larger than the moment arms of passive tissues, which are mostly located around the spinal column. The contribution of intramuscular connective tissue to the resistance to axial rotation should have been minimal under the experimental conditions employed due to the neutral positioning of the subjects. We conclude that the measured torques to imposed twisting in the neck, trunk, and hips reflect primarily the resistance of active muscle contraction and, by inference, the measured torsion torques are closely related to muscle tone.

#### Relation between axial torque and the level of tone

While torque varied by an order of magnitude between the different levels of the axis (Table 1), torque is not a direct measure of muscle tone, because torque depends on the cross-sectional area of the active muscles and their moment arms, in addition to the level of active muscle force. The cross-sectional areas and moment arms of the axial and proximal muscles are impractical to measure directly. Tonic force can be estimated, however, as a function of the known maximal voluntary torque  $T_{\max}$  of the corresponding muscles. The average  $T_{\max}$  of the neck muscles has been estimated at 15 Nm in males and 6 Nm in females (Vasavada et al. 1998). The average  $T_{\max}$  of the trunk muscles has been estimated at 97 Nm in standing males and 60 Nm in females (Kumar and Panjabi 1995; Kumar et al. 2001; McGill and Hoodless 1990; Ng et al., 2001; Perez and Nussbaum 2002). Finally, the average  $T_{\max}$  of internal hip rotation has been estimated to be 60% of that of the trunk in males and 65% in females (Stoll et al. 2000). Based on our torque data (i.e., Table 1), it follows that the tonic force of the neck muscles was  $\sim 6.1\%$  of maximum for males and 4.6% of maximum for females; the tonic force of the trunk muscles was 6.1% of maximum for males and 7.1% of maximum for females; and the tonic force of the hip muscles was 6.8% of maximum for males and 4.2% of maximum for females. Thus assuming that torsional resistance is primarily due to tonic

muscle activity, the relative level of this activity (i.e., muscle tone) appears to have been roughly equal at different levels of the axis, and unlike raw torque, not systematically different for male and female subjects.

#### Lengthening and shortening reactions in human axial and proximal muscles

Our results demonstrate that, in half of the subjects tested, axial muscle stretch evoked a marked decrease in activity in the stretched muscles and an increase in the shortening muscles, consistent with Sherrington's (1909, 1915) description of the lengthening and shortening reactions. In experimental preparations with increased muscular tone (e.g., decerebrate rigidity, first 30 min after decapitation, 1–2 mo after spinal cord transection) (see Sherrington 1909), lengthening and shortening reactions can be observed. In healthy humans, phasic shortening reactions have been described with rapid movements (i.e.,  $> 100^\circ/\text{s}$ ), and in humans with pathological levels of tonic activity, shortening reactions of the tonic type (Andrews et al. 1972, 1973) have been observed (Andrews et al. 1972; Angel 1982b; Bathien et al. 1981; Berardelli and Hallett 1984; Broman 1949; Diener et al. 1987; Denny-Brown 1962; Katz and Rondo 1978; Rademaker 1947; Rondo 1991; Walsh 1976, 1992; Westphal 1880; Xia and Rymer 2004). In this study, we present evidence for both *tonic* reactions in healthy humans, in muscles of both the axis and the upper extremity, and during slow movement, consistent with the maintenance of posture during slow positional changes.

Given the experimental conditions of the present study, it seems unlikely that the lengthening and shortening reactions are related to the stretch reflex. Fast stretching of axial muscles (e.g.,  $100^\circ/\text{s}$ ) can result in a short-latency response, qualitatively indistinguishable from the reflex response of limb muscles (Alexander and Harrison 2002; Beith and Harrison 2004; Colloca and Keller 2001; Granata et al. 2004; Krajcarski et al. 1999; Myrkinas et al. 2000; Stokes et al. 2000; Thomas et al. 1998; Wielder et al. 1996). In the present study, the absence of stretch-evoked muscle activation in all but one subject (see Table 3) is probably due to the velocity employed ( $1^\circ/\text{s}$ ). However, the characteristic of the stretch reflex that most distinguishes it from the responses observed in the present study is that the modulation of muscle activity is oppositely directed to that of the lengthening and shortening reactions.

Half of our subjects did not exhibit lengthening and shortening reactions during axial torsion, similar to a previous study

TABLE 3. Depth of EMG modulation of shoulder muscles (%)

| Subject | Shortening        | Lengthening       | Lengthening       | Shortening        |
|---------|-------------------|-------------------|-------------------|-------------------|
| 1       | 34.00             | 30.80             | 44.60             | 29.30             |
| 2       | 35.10             | 21.70             | 14.10             | 25.20             |
| 3       | 35.90             | 10.40             | 42.60             | 13.70             |
| 4       | 65.90             | 57.00             |                   |                   |
| 5       | 28.60             | 21.50             | 50.80             | 15.20             |
| 6       | 66.10             | 56.70             |                   |                   |
| 7       | 101.50            | 126.00            | 58.30             | 83.90             |
| 8       | 120.30            | 39.80             | 44.80             |                   |
| 9       | 66.60             | 29.40             | 32.70             | 41.30             |
| 10      | 37.50             | 34.50             |                   |                   |
| 11      | 74.20             | 48.10             | 46.70             | 35.10             |
| Average | 60.52 $\pm$ 28.67 | 43.26 $\pm$ 29.68 | 41.83 $\pm$ 13.34 | 34.81 $\pm$ 23.82 |

of transient neck reactions in healthy individuals (Vibert et al. 2001). It is possible, in these latter subjects, that the threshold for eliciting lengthening and shortening reactions was not reached in  $1^\circ/s$ ,  $\pm 10^\circ$  rotations, but it is also possible that there are factors other than unconscious tonic activity required for the development of these reactions. Previous observations of decerebrate animals suggest that the elicitation of lengthening and shortening reactions depends, not on a specific threshold of unconscious muscle activity, but rather a specific intermediate range of tone (Beritoff 1915; Sherrington 1915). Thus there may exist a "window" of central excitability relevant to the maintenance of posture within which lengthening and shortening reactions may be elicited to maintain a compliant interface between the trunk and either forces originating from the extrapersonal environment or from voluntary limb movements.

We presume that the difference between subjects whose postural muscle tone was modulated by axial torsion and those whose activity was not corresponded to differences in the state of the nervous structure controlling muscle tone. Consequently, the presence or absence of tonic lengthening and shortening reactions may reflect the state of this structure, which is highly sensitive to central and peripheral input and which can flexibly regulate the balance between mobility and stability. The postural tone of the axial and proximal muscles, as well as that of the extraocular and orofacial muscles, reflects the underlying tone of the CNS. Correspondingly, studies of postural tone can help us to elucidate the mechanisms of tonic neural activity.

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