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Trunk muscle activity during the simultaneous performance of two motor tasks

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Abstract A unique feature of trunk muscles is that they can be activated to meet functional requirements for combined behaviors, including those related to posture and breathing. Trunk muscles therefore may have developed mechanisms for dealing with simultaneous inputs for different task requirements. This study was designed to test the hypothesis that a linear addition in trunk muscle activities would occur when an isometric trunk task and a pulsed expiration task was performed simultaneously. Surface electromyograms (EMG) were recorded from four trunk regions (medial and lateral back, upper and lower lateral abdomen) in sitting during the performance of the individual isometric trunk task, the individual pressure task, and the combined task (isometric trunk and pressure task). The direction of static holding for the isometric trunk task was varied between flexion and extension positions. For the pressure task subjects produced two consecutive pressure pulses (2/s) to a target oral pressure. For each muscle recording, a linear prediction was calculated from the mathematical addition of the EMG recorded from the individual trunk and pressure tasks. This linear prediction was compared to the actual muscle activity recorded during the combined task. Typically the EMG from two muscles showed linear addition, such that the relative contribution of muscle activity did not change for the combined task. This suggests that the motor commands for each task reached these motor neuron pools essentially unmodified. The other two muscles showed nonlinear combination of two EMG patterns. That is, qualitatively both EMG patterns, specific to each command, were evident in the measured EMG traces for the combined task, but quantitatively the

muscle did not meet all criteria for linear addition. Linear addition may provide a simple mechanism for combining breathing-related behaviors (expiratory efforts) with other trunk behaviors (holding against gravity). This suggests that some muscles can be shared for two different voluntary tasks without changing their contribution to either component task. At the same time, nonlinear combination suggests that some muscles are shared, but their contribution to either component task may be modulated, thus avoiding the construction of a third new and unique plan.

Keywords Trunk muscles · Electromyography · Isometric · Expiratory efforts · Human

Introduction

Trunk muscles have broad anatomical origins and insertions that are linked to several structures; spine, pelvis, rib cage, shoulder girdle. As a result, trunk muscles participate in a wide range of everyday behaviors and meet functional requirements for trunk bending, reaching, locomotion, balancing, breathing, and breathing-related behaviors such as vocalizing. A unique feature of trunk muscles is that they can be activated to meet functional requirements for combined behaviors. These combined behaviors often include everyday tasks, such as the combination of breathing and locomotion. In addition, they can include combinations of highly skilled tasks, such as trunk bending and forced expiration in the marching band horn player. Trunk muscles may therefore be simultaneously activated by two different motor commands for combined behaviors (i.e., move the trunk forwards during marching, generate driving pressures during horn playing). If two sets of motor commands arrive simultaneously at the level of motor neuron (MN) pools, trunk muscle activity during the combined behavior may resemble an addition of the pattern of trunk muscle activity associated with each individual task. This study was designed to test the hypothesis that a lin-

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ear addition in trunk muscle activities would occur when two motor tasks requiring the same musculature (e.g., trunk holding and expiratory efforts) were performed simultaneously.

Several studies suggest, qualitatively that when required to participate in a combined behavior, an individual trunk muscle can contribute activity to both component tasks. For example, when a trunk rotation holding task was combined with quiet breathing, the tonic muscle activity of the external intercostal muscle showed phasic increases coincident with inspiration (Rimmer et al. 1995). In addition, when a trunk flexor holding task was combined with a Valsalva maneuver (voluntary pressurization task), the abdominal muscle activity appeared equal to the tonic level of the holding task plus the tonic level of the Valsalva maneuver (Cresswell and Thorstensson 1989; Cresswell et al. 1992). Similarly, back muscle activity (lumbar erector spinae) related to a lifting task increased when a forward postural perturbation occurred simultaneously (Oddsson et al. 1999). These studies did not test for a linear addition of trunk muscle activities, but their results *qualitatively* suggest that the muscle activation levels in the combined behavior represented an addition of muscle activity related to each individual task.

Other studies, however, quantifying limb muscle activation levels during combined behaviors have reported linear addition of muscle activity related to each individual task (Sergio and Ostry 1994, 1995). The EMG amplitude during a combined behavior of elbow flexion and forearm supination equaled the sum of EMG amplitudes related to each individual task alone. This linear addition of EMG amplitudes occurred, however, only in multiarticular limb muscles, such as the long head of biceps, which were capable of acting as agonists for both component tasks (e.g., flexion and supination). Since trunk muscles have multiple attachments and produce force in several directions, it might be predicted that they would act as multiarticular limb muscles and therefore demonstrate linear addition in a combined behavior. On the other hand, linear addition is not the obvious and only solution for combined trunk behaviors. Several studies suggest that among the synergistic trunk muscles, specific muscles are independently controlled and specialized to meet mechanical requirements for one task more than another (Cresswell et al. 1994; Donisch and Basmajian 1971; Hodges and Richardson 1997, 1999; Hodges et al. 1997; Morris et al. 1962; Oddsson and Thorstensson 1990; Pauly 1966; Strohl et al. 1981). For instance, McGill et al. (1995) showed that erector spinae and abdominal muscles continued to support the spine but made no contribution to respiration during a holding task that was combined with a ventilatory challenge (high CO₂). In another example, lifting-related activity of the erector spinae was turned off when a simultaneous postural disturbance occurred (Oddsson et al. 1999). Thus it is not clear from these studies whether trunk muscles respond linearly during a combined holding and pressure task, similar to multiarticular arm mus-

cles, or whether each trunk muscle has a specialized function, contributing to only one component task of the combined task.

In order to test for linear addition, trunk muscle activity during two motor tasks, antigravity trunk holding and pulsed expiratory efforts, was compared in this study. Each task required activation of the same back and abdominal muscles but with different temporal patterns of EMG activity. The trunk-holding task required a tonic pattern of EMG whereas the pulsed expiratory effort required a phasic pattern of EMG. As a result, each EMG pattern could be clearly distinguished when the two tasks were performed simultaneously. Additionally, each of these tasks, when performed individually, have shown linear or graded EMG-force relationships (Andersson et al. 1977; Bishop 1964; Campbell and Green 1953; Cresswell et al. 1992; Schultz et al. 1982; Sears and Davis 1968; Stokes et al. 1987; Tan et al. 1993). This makes the combined tasks in this study a straightforward test of linear addition. In one experiment the subjects held the trunk in flexion and combined it with pulsed expiratory efforts. In the other experiment the subjects held the trunk in extension and combined it with pulsed expiratory efforts. In this manner the two combined behaviors varied in their effects on intra-abdominal pressure, chest wall shape, and spinal stabilization requirements.

The neural control of trunk muscles during different types of motor tasks probably involves both reflex and automatic mechanisms (Crenna et al. 1987; Cresswell 1994; Oddsson and Thorstensson 1986; Zedka et al. 1999). In addition, clinical and neurophysiological evidence in humans suggests that direct cortical-spinal pathways to trunk muscles coexist with other segmental and descending pathways (Gandevia and Plassman 1988; Gandevia et al. 1990; Munschauer et al. 1991; Severinghaus and Mitchell 1962). The tasks in this study were designed to emphasize descending pathways by requiring subjects to follow specific task instructions regarding trunk angle as well as target pressures, pressure rate, spinal and head alignment, and lung volume. Hence the subject's conscious awareness to each task was increased (e.g., "voluntary" control, Prochazka et al. 2000). To assure consistent performance across tasks, kinematics and oral pressures were quantified and maintained the same during the individual and the simultaneous performances of the two tasks. Thus we could test whether during the simultaneous performance of two tasks trunk muscles were recruited equally (linear addition), were recruited for one task more than another (nonlinear combination), or were recruited for only one task. Results showed that when a subject followed specific task instructions, two muscles showed linear addition, regardless of the direction of holding. That is, their relative contribution of muscle activity to the two component tasks did not change. The other two muscles contributed activity to both component tasks, but muscle activities combined nonlinearly when performed simultaneously. Preliminary results have been presented in abstract form (Farley et al. 1998).

Materials and methods

Six healthy men were recruited for this study from among university students and the local community. The subjects' age, height, and weight ranged from 23 to 29 years, 152 to 177 cm, and 59 to 76 kg, respectively. All subjects were nonsmokers with minimal body fat, had no history of neurological or respiratory disorders and no physical deficits involving the trunk. Fitness levels among subjects were similar, as all subjects participated in a high-intensity exercise program 3–5 days a week. Subjects gave informed consent, and procedures were approved by the Human Subject Committee, in accordance with the ethical standards in the Declaration of Helsinki.

Tasks and procedures

For the trunk task the subject was seated and instructed to hold the trunk isometrically in the sagittal plane at a predetermined angle. In this manner trunk muscles were tonically active to resist the static torques due to gravity (Ortengren and Andersson 1977). Trunk flexors were tonically active in a holding position of trunk extension and vice versa, trunk extensors were tonically active in a holding position of trunk flexion. The specific trunk angles (20° extension, 30° flexion) were selected for two reasons; at these angles, (a) the large mass of the trunk elicited significant EMG activity without the need to add external loads, and (b) trunk muscles would be operating in the middle of their linear EMG-force range (Andersson et al. 1977; Schultz et al. 1982; Stokes et al. 1987; Tan et al. 1993). The target trunk angle was controlled by requiring the subject to bend until his trunk made light physical contact with a dense foam wedge, set at a height and distance to ensure that the subject achieved the desired target trunk angle. In this task the foam wedge did not support the weight of the trunk but provided a physical cue so that subjects maintained a straight spine and held the trunk in the sagittal plane without rotating their shoulders (confirmed in pilot studies). Although pressure of the light contact was not measured, investigators were assured that subjects did not rest their trunk on the wedge because any change in trunk angle or EMG was monitored (see "Determining acceptable trials").

For the pressure task the subject was seated and instructed to make two expiratory efforts against a partially obstructed mouthpiece. Previous studies (Cresswell and Thorstensson 1989; Cresswell et al. 1992; Goldman et al. 1987) and pilot work showed that this type of task elicited phasic coactivation of abdominal and back muscles. The coactivation increases intra-abdominal pressure, which provides a platform against which the rib cage can operate for generating expiratory pressures (Grassino and Goldman 1986; Milic-Emili 1964). It is known that when subjects produce rapid expiratory efforts at a rate faster than 4 Hz, trunk muscles become tonically active (Stetson 1951). At slower rates, however, phasic bursts of trunk muscles occur. Since a phasic burst pattern was desired in order to contrast with the tonic holding pattern, the subject was instructed to make two equal and evenly timed efforts within 1 s. A metronome indicated the 1-s timing, and subjects self-paced the two efforts within each beat of the metronome. Two vs. single expiratory efforts were used because this required greater skill of the subjects and represented a greater difference in EMG pattern from the tonic holding pattern.

Lung volume changes were minimized by partially obstructing the airway (mouthpiece and noseclips) and keeping trials short (1 s). The expiratory efforts were matched to a target oral pressure (P_O) established for each subject. Target P_O values ranged from 30 to 50 cmH₂O across subjects, which represents about 40% of maximal and is within the middle of the linear EMG-force range for the abdominal muscles (Campbell and Green 1953). In this task the subject performed the pressure task with the trunk fully supported on the dense foam wedge, reclined either backward or forward to match the target trunk angle required for the isometric trunk task. Full support was verified by online monitoring of resting EMG levels prior to each trial.

For the combined task the subject performed both the trunk task and the pressure task simultaneously. The same parameters were set as required in the individual tasks (i.e., trunk angle, target P_O , and pulse rate). Thus the subject was instructed to lean backward or forward until his trunk made light physical contact with the foam wedge and to actively hold his trunk at this angle, while performing two consecutive pulsed expiratory efforts at a rate of 2/s to the target P_O .

Each experiment included ten trials for each of the three different tasks, which were always performed in the same order: the holding task, the pressure task, and the combined task. At the beginning of a trial the subject exhaled to resting-expiratory level (REL), stopped breathing, and assumed the target trunk position (leaning backward or forward). The purpose of breathholding at REL was to control the influence of lung volume and/or respiratory cycle on the threshold of recruitment and activity levels in trunk muscles (Bishop 1964; Cala et al. 1992; Fregosi et al. 1990; Hodges et al. 1997; Rimmer et al. 1995; Tokizane et al. 1952).

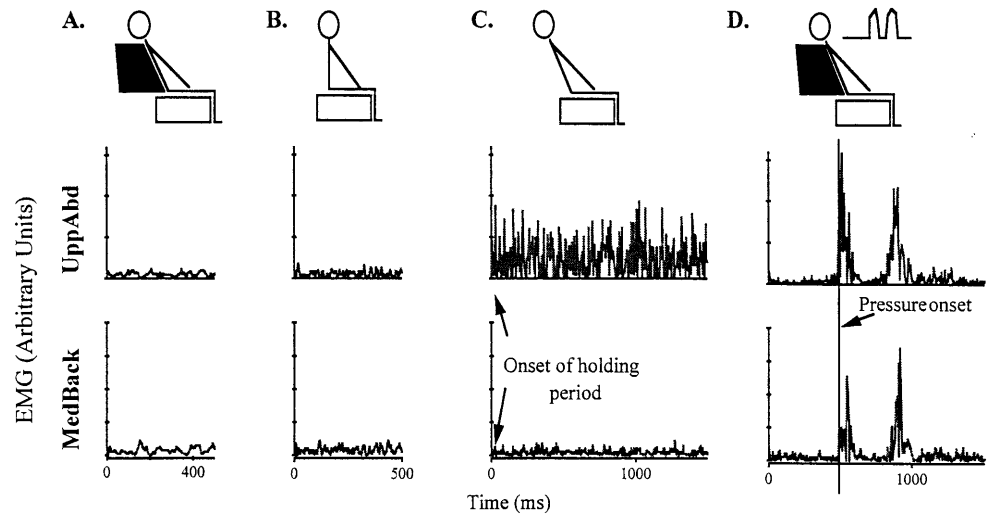
Data collection

P_O was sensed with a catheter inserted through a mouthpiece and behind the lips, connected at the other end to a pressure transducer (Validyne MP45-871, Northridge, Calif., USA) and amplified (Validyne PS238). The opening of the mouthpiece was partially obstructed with a cork, which contained a small hole designed to guard against the subject "puffing" his cheeks to raise P_O . In addition, the pressure signal was displayed on an oscilloscope (Tektronix Type 565, Beaverton, Ore., USA) to provide visual feedback to the subject to assist in producing the target P_O . A manometer was used to calibrate the signal at the end of each session.

Bipolar surface electrodes (10 mm diameter, 2 cm interelectrode distance) were used to record muscle activity from four regions: two on the back and two on the abdomen. Data were collected from one side of the body because no significant differences have been found in muscle activation between right and left sides in symmetrical sagittal plane postures or movements (Andersson et al. 1977; Jonsson 1970; Schultz et al. 1982; Seroussi and Pope 1987; pilot work). There is evidence that trunk muscles generate force cooperatively through attachments into fascia, such that different parts of the same muscle as well as synergists in the same region may be activated differentially (Gracovetsky 1990; Macintosh et al. 1987; McGill and Norman 1988; Tesh et al. 1987). In addition, trunk muscles are often broad, such that multiple intramuscular electrodes would be required to capture regional changes in muscle activity within a single muscle. Considering these structural and functional aspects of trunk muscles, surface electrodes were considered more appropriate for the purpose of this study to detect changes in EMG from a large muscle volume. To maximize signal detection to the most superficial underlying muscles the location of surface electrodes was carefully chosen from other studies that used ultrasound-guided intramuscular recordings (Cresswell et al. 1992; Strohl et al. 1981) or that compared intramuscular and surface recordings (Andersson et al. 1974; Hodges and Richardson 1997). Furthermore, electrodes at each location were positioned on top of, and in line with, the orientation of fibers of the most superficial muscle in that region.

To monitor back muscle activity, EMG was recorded from medial and lateral locations in the lumbar region of the back. Electrodes for the medial location (MedBack) were placed at the L4-L5 interspace, as defined by the vertebral spinous process 2 cm lateral from the midline (Hodges and Richardson 1997) over the multifidus muscle, covered only by the tendinous origin of the erector spinae muscle fibers. The electrodes for the lateral back location (LatBack) were placed at L3 6 cm lateral from the midline (Anderson et al. 1974) over the iliocostalis lumborum as the most superficial muscle. To monitor abdominal muscle activity EMG was recorded from an upper and lower location on the lateral abdomen. Electrodes for the upper lateral abdominal location (UppAbd) were placed midway between the anterior superior iliac spine (ASIS) and the caudal border of the rib cage, over the external oblique as the most superficial muscle (Cresswell and

Fig. 1A–D Individual trials of raw, rectified EMG data from two muscles under different conditions: during two relaxed positions, supported in extension (A) and upright sitting (B), and during two different individual tasks; the holding in extension task (C) and the pressure task with supported sitting (D). ECG signals were removed only from these segments of the data used for analysis. For each muscle scales are the same across all four comparisons (arbitrary units). Resting levels (taken from A) have been subtracted from C and D. Vertical line (D) denotes pressure onset



Thorstensson 1989). Even though the internal oblique and transversus abdominus fibers underlie the external oblique, their fibers run perpendicular to the external oblique, reducing the influence of volume conduction. Finally, the electrodes for the lower lateral abdominal location (LowAbd) were placed 3 cm medial and 3 cm inferior to the ASIS (Cresswell 1993; Cresswell and Thorstensson 1989) over the internal oblique muscle, covered only by the external oblique aponeurosis (Floyd and Silver 1950; Strohl et al. 1981). It is possible that the transversus abdominus muscle contributed to the activity recorded from the LowAbd location as in some subjects these fibers may lie under the internal oblique muscle; however, volume conduction is considered low in this area (Carman et al. 1972; Floyd and Silver 1950). Activity was recorded from the lateral abdominal muscles (upper and lower) but not from the rectus abdominus muscle because pilot work and other studies have shown that phasic expiratory activity is consistent in the lateral abdominal muscles but inconsistent and observed only at maximal efforts in the rectus abdominus (Abe et al. 1996; Strohl et al. 1981; Tokizane et al. 1952).

Data analyses

Determining acceptable trials

Trials were selected for EMG analysis if they met kinematic and P_O criteria. Subjects were required to maintain the designated target trunk position without moving head or extremities and to produce the correct pressure template. The investigator and two assistants qualitatively assessed the kinematic and pressure criteria at the time of data collection and again later assessed videotapes. To assure that subjects were not varying their level of support throughout a trial, trials were eliminated if the trunk angle deviated from the established position by $\pm 5^\circ$. EMG was also monitored online to eliminate trials during the pressure task if initial resting EMG levels changed. During the holding task trials were eliminated if initial tonic EMG levels were not consistent and of appropriate amplitude for holding without support. Trials with pulsed expiratory efforts were eliminated if pressure pulses were not completed within 800–1200 ms. Trials were also rejected if the two peak P_O signals fell outside ± 5 cmH₂O of the target P_O or if the minimum P_O signal between the two peaks failed to decrease to 15 cmH₂O or less.

Analysis of EMG

EMG signals, sampled at 200 Hz, were amplified (Grass 7P511, Quincy, Mass., USA) and filtered (bandpass 10–1000 Hz). The

electrocardiographic (ECG) signal was subtracted from the raw EMG records, and EMG records were then rectified. Individual trials were smoothed and averaged. Holding tasks were aligned by the start of the holding period, determined by an event marker (Fig. 1C). The pressure tasks and combined tasks were aligned by P_O onset (Fig. 1D). Finally, for each subject and muscle the averaged, smoothed EMG records were normalized to the largest peak amplitude recorded from either experiment (Cresswell et al. 1992, 1993; Thorstensson et al. 1985). These smoothed, averaged, and normalized EMG records are referred to here as EMG traces.

Trunk muscles often exhibit tonic activity during relaxed positions. This made it necessary to establish a level of EMG at rest. In Fig. 1 the EMG levels during two different relaxed conditions are illustrated, supported on the foam wedge in the extension position (Fig. 1A) and sitting upright (Fig. 1B). Levels of EMG were reduced for both relaxed conditions in comparison to the task of actively holding the trunk (Fig. 1C). The lowest levels of EMG activity consistently occurred in the supported condition for all subjects. As a result, an average amplitude was determined during a 50-ms window from the EMG trace during the supported condition. This resting level was then subtracted from the EMG traces so that only activity above this baseline was further analyzed. Occasionally a subject showed activity levels in muscles during a task that were below resting levels, resulting in negative EMG values.

Determination of linear addition

To determine whether the EMG recorded during the combined task represented a true addition of the EMG associated with the two individual tasks a mathematical model of an EMG trace representing a strict linear addition was produced. That is, a point-to-point addition of the EMG traces from the individual trunk task and the individual pressure task was executed (Fig. 2), resulting in a new trace called the predicted trace. This predicted EMG trace was then superimposed with the EMG trace that was recorded during the combined task (called the measured trace). Qualitatively, if the two individual EMG patterns were both evident in the measured trace and represented a linear addition, the superimposed traces (measured and predicted traces) should perfectly match. Quantitative procedures were performed to determine how similar the two traces were to one another. Scatterplots were first constructed by plotting the two traces and calculating Pearson's correlation. The correlation coefficient (r) was calculated and squared (r^2) to describe the proportion of moment to moment variation in the predicted trace that could account for the variation in the measured trace. If the shape of the measured trace exactly matched the predicted trace, the data would fit a straight line, with a $r^2=1.00$.

Fig. 2A,B Mathematical model for quantifying linear addition. This schematic illustrates the point-to-point addition of averaged EMG traces for an abdominal muscle (LowAbd) from the two individual tasks (holding in extension and pulsed expiratory efforts), resulting in a new trace called the predicted trace

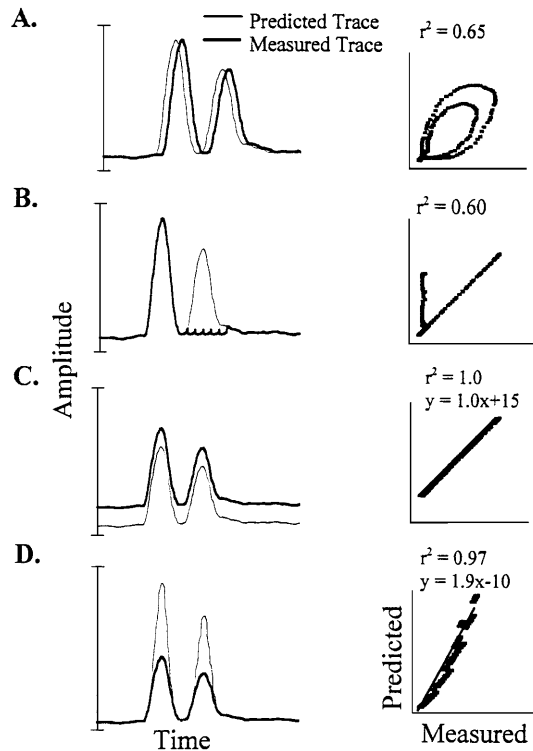
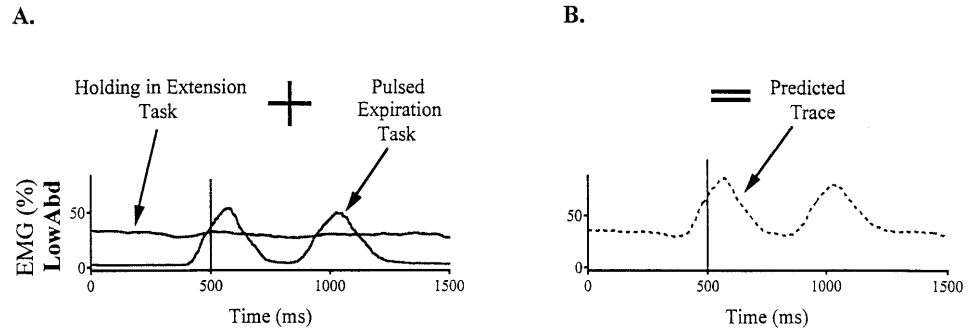


Fig. 3A–D This figure illustrates the sensitivity of point-to-point correlations between two hypothetical traces, mimicking the measured and predicted EMG traces. *Thin line* predicted trace; *dark line* measured trace. The two traces are overlaid on the left, and their corresponding scatterplots and r^2 values are shown on the right. Each trace on the left illustrates a different variation in the measured trace that could be reflected in the correlation plot. **A** The traces are the same except for the measured trace is delayed 50 ms in reference to the predicted trace. This produced a plot with broadening of the data into circular patterns, and a low r^2 value (0.65). **B** An obvious shape difference (the measured trace is missing the second phasic burst) also produced a low r^2 value (0.60). **C** Initial tonic levels are increased in the measured trace. **D** Peak amplitudes are decreased in the measured trace. In both of these correlations, the r^2 value continues to be high (1.0 and 0.97), but the data points are shifted along the y-axis (C) or no longer fall along a slope of 1.0 (D)

The sensitivity of this method is illustrated in several hypothetical correlations in Fig. 3. For instance, if the two traces are similar in shape, but the relative timing of the pressure-related bursts in one trace is delayed in relation to the other, the data in the scatterplot widens into circular patterns, and r^2 is reduced (Fig. 3A). If the two traces are similar in timing but are different in shape (for

instance, one trace fails to produce a second phasic burst), the r^2 is reduced (Fig. 3B). If however, traces are similar in shape and timing, but one trace shows differences in initial tonic levels, the r^2 continues to be high but the data points are shifted along the y-axis and offset vary from 0 (Fig. 3C). Similarly, if traces are similar in shape and timing, but peak amplitudes differ, the data points no longer follow a line with a slope of 1 (Fig. 3D). This indicates that the r^2 value provides an indicator for overall similarity in shape and timing, but alone it cannot distinguish differences in amplitudes (e.g., initial tonic levels or peak amplitudes). To determine similarity in amplitudes a one-sample t test was to determine whether the values for the offset and slope differed with statistical significance from 0 or 1.0, respectively.

Results

Experiment 1: holding in extension + pulsed expiratory efforts

The three tasks of this experiment are shown in Fig. 4. For the individual trunk task subjects held the trunk in 20° of extension (Fig. 4A). The holding muscles (UppAbd and LowAbd) were tonically active for the duration of the holding period. Activity levels for the non-holding muscles (MedBack and LatBack) were typically negligible. During the individual pressure task (Fig. 4B) two distinct EMG bursts occurred in all muscles coincident with each pressure pulse. Onsets of EMG bursts occurred 100 ms in advance of the onsets of pressure pulses. EMG was negligible prior to and after each burst. During the combined task the pattern of EMG activity resembled both individual patterns (Fig. 4C). For the abdominal muscles (UppAbd and LowAbd) two pressure-related bursts occurred on top of a tonic level of activity required to hold the trunk. For the back muscles (LatBack and MedBack), two pressure-related bursts occurred on top of minimal or negligible levels of tonic activity that were similar to the levels of activity in the individual trunk task (holding in extension, see Fig. 4A).

A comparison of EMG activity from the combined task (measured EMG trace) to the mathematical addition of EMG activity from the two individual tasks (predicted EMG trace) is shown for a representative subject in Fig. 5A. The shape and timing of the measured trace generally resembled the predicted trace for each muscle. This indicates, qualitatively that both task-specific EMG

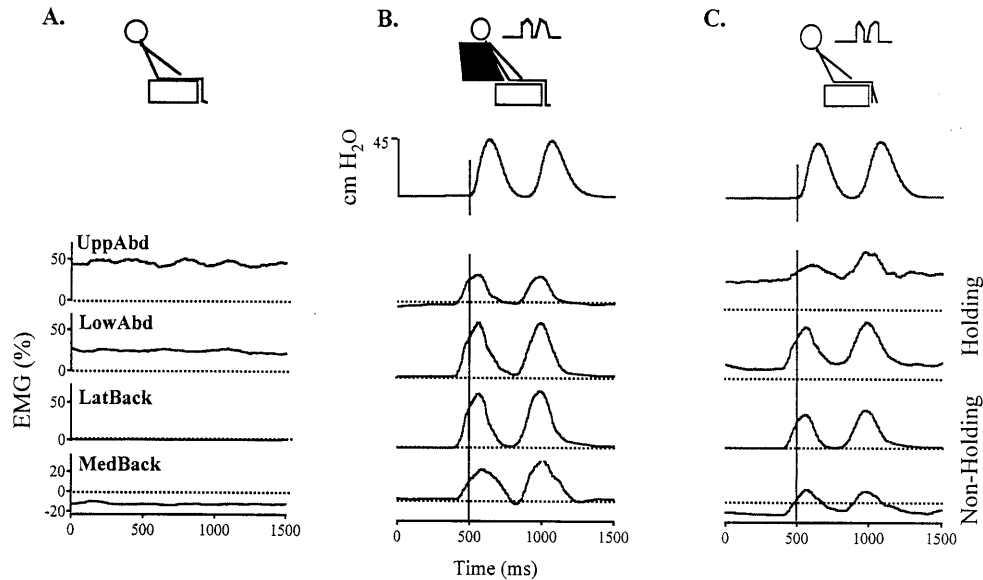
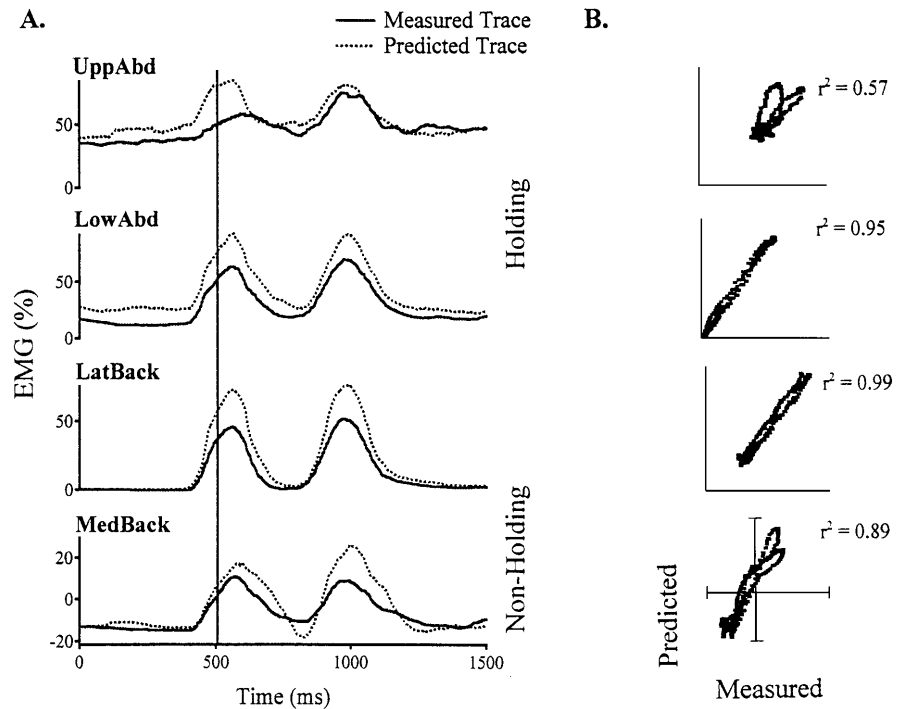


Fig. 4A–C EMG traces representative of each of the three tasks in Experiment 1. **A** Holding in extension task. **B** Pressure task. **C** Combined task. *Top trace* (in tasks **B**, **C**) the pressure trace; pressure onset is identified across traces by the *solid vertical line*. *The next four traces* (and all traces in **A**) are averaged EMG traces from the two abdominal muscles (holding) and two back muscles (nonholding). Units are relative to the largest amplitude recorded

across all tasks in either isometric experiment. *Dotted line* zero baseline. *Figures at top* illustrate the task conditions for the three tasks: holding task with unsupported sitting (**A**), pressure task with supported sitting (**B**), and holding plus pressure tasks with unsupported sitting (**C**). For each muscle, amplitudes are scaled the same for all three tasks. Data are from subject 5

Fig. 5A,B Comparisons of measured vs. predicted traces for one subject (S5). *Dark line* measured trace; *dotted line* predicted trace. All traces are aligned by pressure onset denoted by the *solid vertical line*. *On the left* comparisons for each muscle for one subject are shown in **A**, with the corresponding scatterplots and r^2 values *on the right* in **B**. Each scatterplot is composed of 300 correlated data points from the two EMG traces on the left. Values of r^2 ranged from 0.57–0.99



patterns were evident in the measured trace. Scatterplots and r^2 values of the measured vs. predicted traces are shown to the right in Fig. 5. The scatterplots demonstrated linear relationships, with a slope close to 1.0 for three of the four muscles. These same three muscles demonstrated high r^2 values (0.89–0.99). One holding muscle, UppAbd, showed loops in the scatterplot with a low r^2

value (0.57) coincident with the timing differences, particularly evident in the first pressure-related burst.

A cutoff value for r^2 was needed to indicate that the two EMG traces (predicted and measured) were quantitatively the same shape and timing. As a result, a frequency distribution of all r^2 values for both experiments of this study was generated (Fig. 6). Using a total of

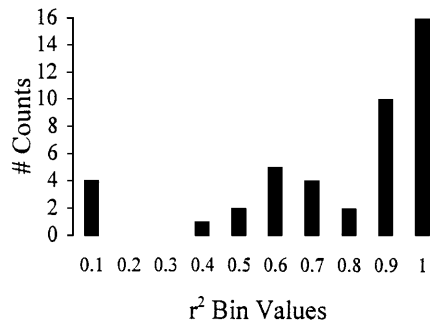


Fig. 6 Frequency distribution of r^2 values across both isometric experiments ($n=43$). Values of r^2 showed a bimodal distribution; one with a major grouping with a peak at 1.0, a break at 0.8, and a minor grouping with a peak at 0.6

43 r^2 values, a bimodal distribution of r^2 values occurred with a large peak at 1.0 and a smaller peak at 0.6. A cut-off value was chosen at the break between peaks, thus r^2 needed to be equal or greater than 0.8. For the representative subject in Fig. 5, three of the four muscles met the r^2 criterion of being 0.8 or greater (LowAbd, LatBack, MedBack) indicating that shape and timing was essentially the same between EMG traces. In the remaining muscle (UppAbd, a holding muscle) the r^2 did not meet criterion reflecting the timing difference in the first pressure-related burst.

Despite high r^2 values in three out of four comparisons for the representative subject in Fig. 5, amplitude differences occurred in the initial tonic levels and peak amplitudes that were not reflected in the r^2 value. This was predicted from the hypothetical correlations in Fig. 3C and D. Statistical comparisons of measured and predicted EMG traces were therefore performed for each muscle across subjects. Such comparisons for two muscles are shown in Fig. 7. For the holding muscle LowAbd (Fig. 7A, B), r^2 values occurred above criterion (0.8–0.96) in all subjects (5/5). Even though differences in initial tonic levels of EMG were apparent in Fig. 7 (S5 and S6), offsets were not significantly different from 0. Similarly, even though differences in peak amplitudes of phasic bursts occurred (S4, S5, S6), slopes of the regressions were not significantly different from 1.0. For the nonholding muscle LatBack (Fig. 7C, D) r^2 values also occurred above criterion (0.83–0.99) in all subjects (6/6), and offsets were not significantly different from 0. Slopes, however, were significantly different from 1.0. Note that for both muscles in Fig. 7 offsets were not significantly different from 0. Therefore the graphical differences in initial tonic levels shown in Fig. 7 (e.g., S5 in Fig. 7A and S2 in Fig. 7B) were not significant and exaggerated differences in peak amplitudes of the pressure-related bursts.

Results for all muscle comparisons in experiment 1 are summarized in Table 1. Cells marked by an asterisk denote EMG traces that met the criterion ($r^2 \geq 0.8$). A summary of findings from statistical comparison for offset and slopes are shown at the bottom of the table. Mus-

Table 1 Summary of linear addition across muscles: holding in extension (experiment 1). – unavailable data; / not tested due to low correlations across subjects; NS not significant; S significant

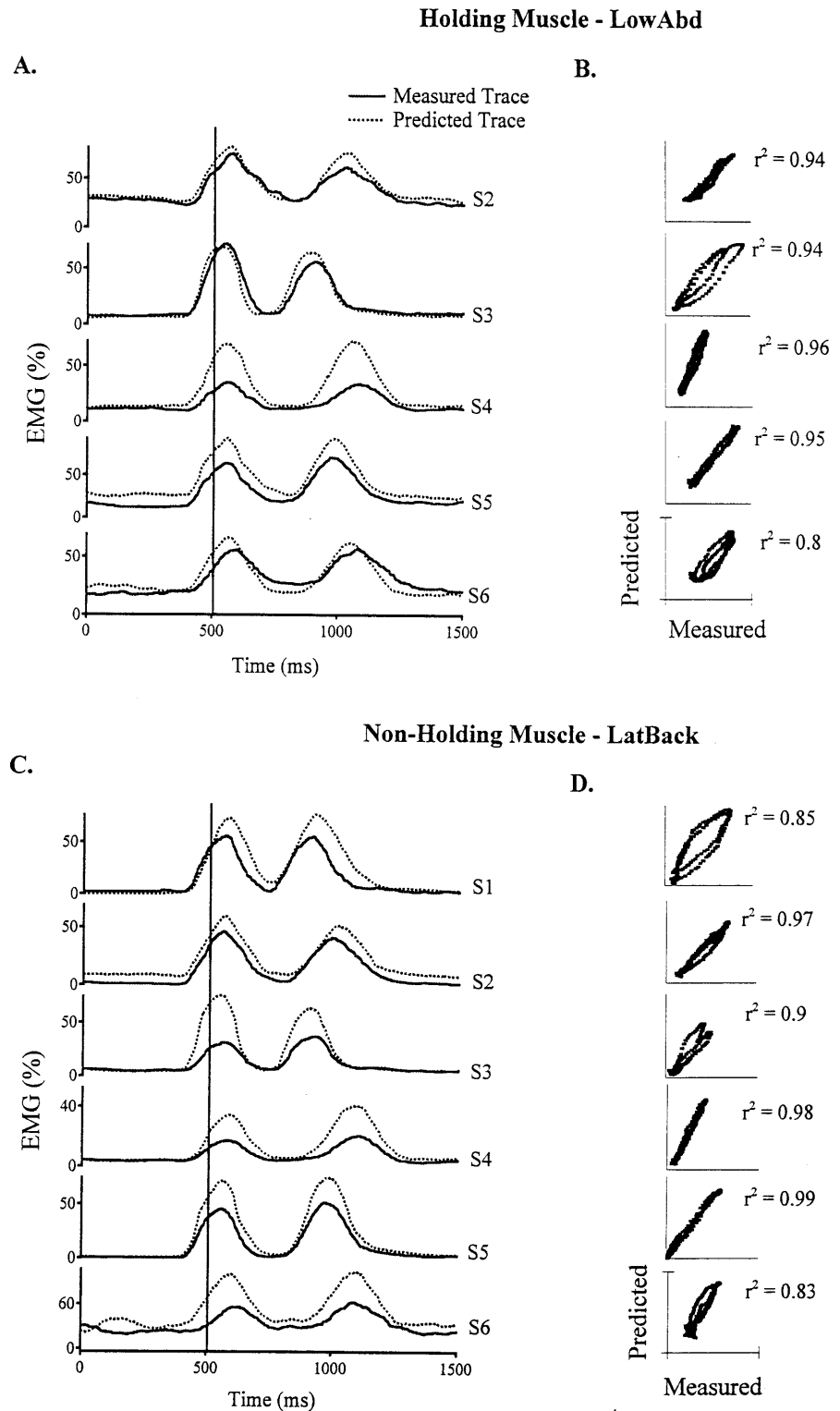
Subject	Holding muscles		Nonholding muscles	
	UppAbd	LowAbd	LatBack	MedBack
1	0.07	–	0.85*	–
2	0.05	0.94*	0.97*	0.88*
3	0.42	0.94*	0.9*	0.94*
4	0.41	0.96*	0.98*	–
5	0.57	0.95*	0.99*	0.89*
6	0.66	0.8*	0.83*	0.52
Offset	/	NS	NS	NS
Slope	/	NS	S	NS
	Nonlinear	Linear	Nonlinear	Linear

cles were categorized as exhibiting linear addition of EMG patterns if it met three criteria, r^2 values 0.8 or higher in the majority of subjects, and no statistical difference in offsets and slopes. Two muscles met all three criteria for linear addition of EMG patterns; a holding muscle (LowAbd) and a nonholding muscle (MedBack). These two muscles therefore had r^2 values 0.8 or higher in the majority of the subjects (100% and 75%, respectively) and no significant differences in offsets or slopes. For the remaining two muscles a nonlinear combination of two EMG patterns occurred. That is, for the nonholding muscle (LatBack), r^2 values were 0.8 or higher in the majority of the subjects (100%), but significant differences in slopes occurred across subjects. For the holding muscle (UppAbd) the r^2 values were below criterion for all subjects. Despite the low r^2 values for this muscle subjects qualitatively showed evidence of both individual patterns in the EMG traces of the combined task (see Fig. 5A, B).

Experiment 2: holding in flexion + pulsed expiratory efforts

The three tasks of this experiment are shown in Fig. 8. For the individual trunk task subjects held the trunk in 30° of flexion (Fig. 8A). All subjects showed an increase in activity in at least one of the holding muscles (LatBack or MedBack). Activity levels for nonholding muscles (UppAbd and LowAbd) were typically negligible. The pattern of pressure-related EMG activity (Fig. 8B) was the same as in experiment 1. Thus, even with the trunk supported in flexion, two distinct coactive bursts occurred in abdominal muscles, coincident with the two pressure pulses. For the back muscles (LatBack and MedBack) EMG patterns varied among subjects and were best appreciated in the MedBack. Two subjects showed the typical phasic increase in activity with each pressure pulse similar to the LatBack in Fig. 8B. For two other subjects the MedBack showed phasic decreases in activity with each pressure pulse as shown in Fig. 8B. The one other subject showed essentially no pressure-related activity in either the

Fig. 7 Comparisons of measured vs. predicted traces for a holding muscle (LowAbd) in (A) and a nonholding muscle (LatBack) in (C) across subjects. Same format as in Fig. 5. The comparisons are shown *on the left* with the corresponding scatterplots and r^2 values *on the right* (C, D). Values of r^2 ranged from 0.80–0.99



LatBack or MedBack (not shown). Despite the intersubject variability in pressure-related patterns for back muscles, each subject maintained his same pattern in the combined task that he had demonstrated in the individual pressure task (see Fig. 8B, C).

A comparison of measured traces to the predicted traces from a representative subject is shown in Fig. 9.

The two traces closely follow each other. For three of the four muscles the correlation of measured to predicted traces demonstrated a linear relationship, with r^2 values ranging above criterion from 0.95–0.97, indicating that shape and timing were essentially the same between EMG traces. The MedBack showed a significant difference in shape and timing as reflected in a low r^2 value

Fig. 8A–C EMG traces representative of each of the three tasks for experiment 2. **A** Holding in flexion task. **B** Pressure task. **C** Combined task. Same format as Fig. 4. Data are from subject 5

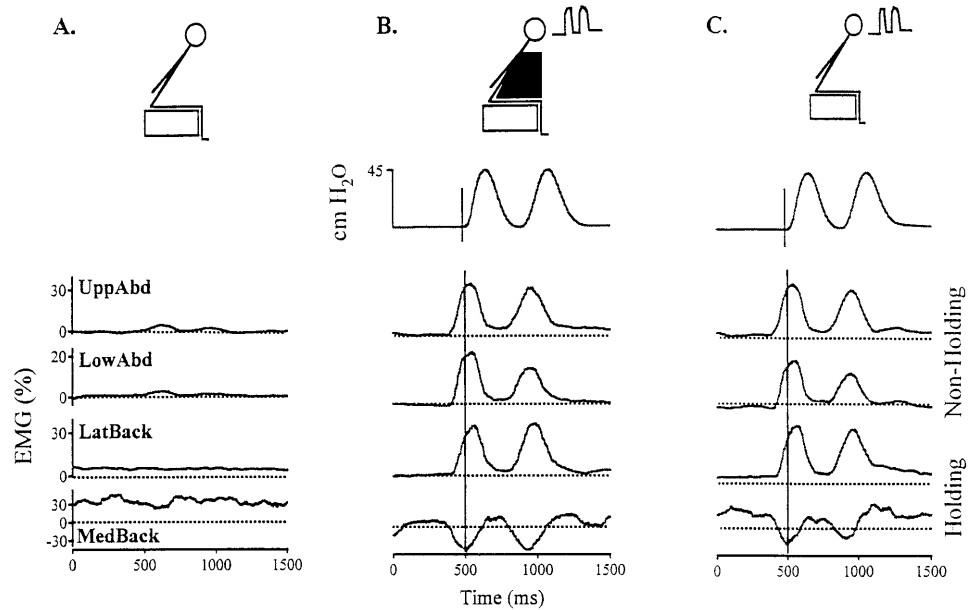
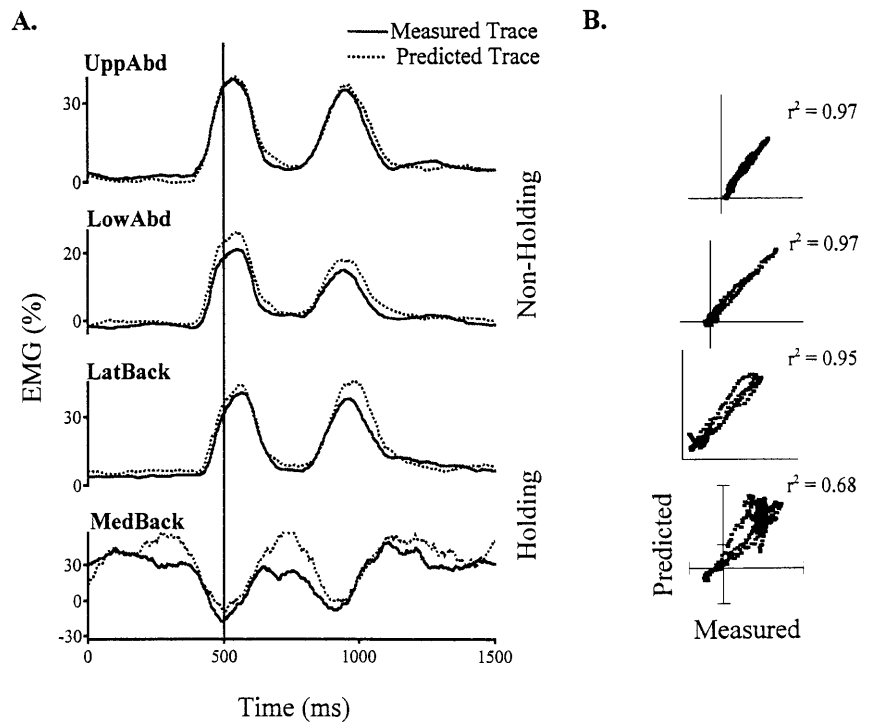


Fig. 9A,B Comparisons of measured vs. predicted traces for one subject. Same format as Fig. 5. *On the left in A* are the comparisons across all muscles for one subject with the corresponding scatterplots and r^2 values *on the right in B*. Values of r^2 ranged from 0.68–0.97. Same subject as in Fig. 8 (S5)



(0.68) although both holding and pressure-related patterns were evident. For all muscles both initial tonic levels and peak amplitudes were closely matched. Consistent with these observations, offsets and slopes of the regressions for each muscle were not statistically different from 0 and 1.0, respectively.

Results for all muscle comparisons in experiment 2 are summarized in Table 2. Since amplitude differences (offsets and slopes) did not occur in this experiment, a muscle had only to meet the r^2 criterion ($r^2 \geq 0.80$ in the majority of subjects) to be categorized as exhibiting linear addition of two EMG patterns. Only two muscles,

both abdominal nonholding muscles (UppAbd, LowAbd), met this criterion. For one of the holding muscles (LatBack) only two of five subjects met the r^2 criterion. For the other holding muscle (MedBack) no subjects met r^2 criterion, a finding that was similar to that of the UppAbd in experiment 1 (Table 1). Also in this experiment one subject (S4) showed r^2 values equal to zero for both back muscles (MedBack, LatBack). This subject showed relatively no pressure-related activity during either the individual pressure task or the combined task in the back muscles. This means that this subject did not use these muscles to produce expiratory efforts and the predicted

Table 2 Summary of linear addition across muscles: holding in flexion (experiment 2). – unavailable data; / not tested due to low correlations across subjects; NS not significant; S significant

Subject	Nonholding muscles		Holding muscles	
	UppAbd	LowAbd	LatBack	MedBack
1	0.96*	NR	0.7	NR
2	0.88*	0.82*	0.52	0.65
3	0.81*	0.92*	0.95*	0.53
4	0.68	0.59	0 ^a	0
5	0.97*	0.97*	0.95*	0.68
6	0.7	0.87*	0.28	0.31
Offset	NS	NS	/	/
Slope	NS	NS	/	/
	Linear	Linear	Nonlinear	Nonlinear

^a resulted from the correlation of two flat tracers

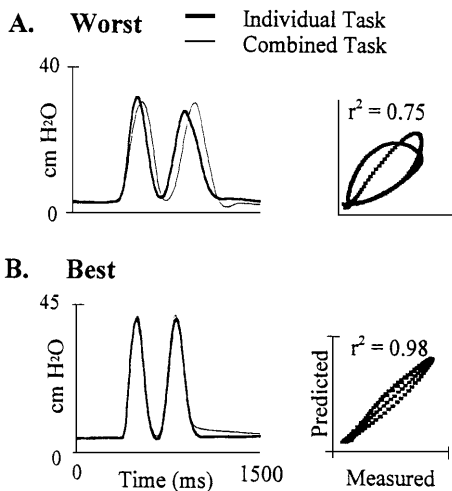


Fig. 10A,B Altered timing of the pressure pulses. A comparison of pressure traces from the individual pressure task (*dark line*) and the combined task (*thin line*) are shown next to their correlation plots for a subject with the worst (**A**) and best (**B**) timing. Both subjects performed within the pressure criteria (± 5 cmH₂O, 800–1200 ms duration). For the subject in **A** large circular loops occurred in the scatterplot, and the r^2 values was low at 0.75. This was in contrast to the subject in **B**, to the four other subjects of this experiment, and all subjects from the previous experiment. Their pressure traces matched almost perfectly and r^2 values were all 0.92 or higher

trace and the measured trace (both flat) represented only holding-related activity.

As indicated by the number of cells with asterisks in Tables 1 and 2, there were more comparisons with r^2 values 0.8 or higher in experiment 1 than in experiment 2. In addition, in experiment 1, subjects tended to only show low r^2 values in one muscle consistently (UppAbd). In Experiment 2 not only did one muscle show low r^2 values consistently (MedBack), but two subjects (S4 and S6) showed low r^2 values across almost all muscles. To determine whether the low r^2 values in these subjects were a result of altered timing of the pressure pulse during the combined task, the trace of the pressure pulse during the combined task was overlaid with the

trace of the pressure pulse during the individual pressure task, and the correlation between the two traces was calculated. Results of this analysis for all subjects in both experiments revealed that these two subjects altered the performance of the pressure pulse during the combined task, delaying the time of the pressure pulses, despite adequately fulfilling the peak pressure (± 5 cmH₂O) and general timing criteria (800–1200 ms duration). This was in contrast to the four other subjects of this experiment and all subjects from the previous experiment, whose correlations showed no change in the performance of the pressure pulses during the combined task vs. the individual pressure task.

The delay in timing of pressure pulses for subject 4 is illustrated in Fig. 10A. For this atypical subject large circular loops occurred in the scatterplot and the r^2 value was low at 0.75 (Fig. 10A). A figure of pressure pulses for one typical subject with appropriate timing is illustrated in Fig. 10B. The pressure traces matched almost perfectly, and r^2 values were all 0.92 or higher. Comparison of the measured and predicted EMG traces for the atypical subject looked similar to the comparison of pressure pulses. That is, the EMG pattern of the measured trace closely resembled the predicted trace but was shifted later. This means that the low r^2 values for subjects 4 and 6 in Table 2 primarily reflected the altered performance of the combined task. Interestingly, one of the subjects with this timing difficulty (S4), was the same one who did not use either back muscle for expiratory efforts (as indicated by the “0” r^2 values for S4, Table 1).

Discussion

Linear addition

The overall results showed that during the combined task not only were both task-specific muscle activity patterns generally evident in all muscles, but in certain trunk muscles the activities were combined by linear addition. A linear addition of muscle activity patterns implies that the trunk muscles are simultaneously activated by two different commands. Evidence for “superimposition” of motor commands has also been demonstrated during elbow flexion and supination tasks (Sergio and Ostry 1995). Previous studies have shown that trunk muscle MN pools receive cortical inputs during instructed (referred to as voluntary) trunk and breathing tasks (Adams et al. 1989; Gandevia and Plassman 1988; Gandevia et al. 1990). In addition, high-level cortical structures (premotor cortex, supplementary motor area, primary motor cortex) are similarly involved in voluntary trunk and breathing tasks as in limb tasks (Macefield and Gandevia 1991; Ramsey et al. 1993). This suggests that two different plans are generated simultaneously, which has been previously suggested to occur for individual degrees of arm motion (Laquaniti and Soechting 1982; Sergio and Ostry 1995; Soechting and Flanders 1993). The present

study suggests that at the final stage of EMG, trunk muscles are able to respond to simultaneous commands, which may represent plans, through an addition of muscle activities.

Each task of this study most likely involves a combination of spinal, automatic, and cortical mechanisms, and hence the input to trunk MN pools probably arises from several anatomical sources. Moreover, it is not known whether the descending input during combined tasks remain separate or blend before reaching the MN pools. Nonetheless, there are two hypotheses about MN pool organization that could account for linear addition at the spinal level. Descending inputs for two different tasks may each have widespread and equal access to the same MN pools, consistent with the general theory of the size principle of recruitment, resulting in the generally increased recruitment of MNs for combined tasks (Henneman et al. 1964; Stuart and Enoka 1983). Indeed, studies of trunk and limb muscles have shown that the same two motor units are recruited for multiple tasks, but that differences exist in the degree of synchronization across tasks (Adams et al. 1989; Bremner et al. 1991). This suggests that there is a differential distribution of inputs for different tasks within a MN pool. Linear addition in this case would result from the increased recruitment of the entire MN pool.

On the other hand, the second hypothesis proposes that two descending inputs preferentially synapse on functionally distinct subdivisions within individual MN pools (Hoffer et al. 1987; Kandou and Kernell 1986), resulting in task-specific recruitment of MNs for combined tasks. Puckree et al. (1988) showed that different abdominal motor units are recruited for two different voluntary tasks (leg lift vs. forced expiration). Similarly, different populations of motor units have been identified in the biceps muscle for elbow flexion vs. supination, with a third subpopulation of motor units related to the combination of flexion and supination (ter Haar Romeny et al. 1984; van Zuylen et al. 1988). Although this is evidence for subpopulations of motor units, it is not known whether they are recruited independently during a combined behavior. Nonetheless, linear addition of EMG patterns would result if subpopulations of motor units were recruited for each component task of a combined behavior. In summary, linear addition could be plausibly explained by either additive recruitment of individual MNs or additive recruitment of subpopulations of MNs within a MN pool.

The finding of linear addition may not occur in all combined tasks but may have occurred in this study as a result of the mechanical compatibility of the two motor tasks chosen for investigation. During the pressure task, abdominal and back muscles were activated in a synchronous pattern. The accompanying increase in intra-abdominal pressure resulting from this coactivation (Cresswell and Thorstensson 1989), although not measured in this study, may have contributed functionally to both of the component tasks during the combined task. For example, it may have stabilized the lumbar spine

during holding (Cresswell et al. 1994; Tesh et al. 1987) and simultaneously contributed to diaphragm and thoracic kinetics during the expiratory efforts (Grassino and Goldman 1986). Therefore the linear addition found in this study may be unique to the ability of trunk muscles to generate intra-abdominal pressures in a manner that does not mechanically interfere with other task goals.

The mechanical compatibility of the tasks investigated in this study is further supported by other evidence that linear addition does not occur when mechanical conflicts exist. For example, back muscles required for a trunk lifting task were found to turn off briefly to allow the abdominal muscles to flex the trunk forward in response to a backward perturbation (Oddsson et al. 1999). This suggests that when conflicting requirements occur, the central nervous system prioritizes inputs to MN pools, allowing muscle activities to switch or alternate between two tasks. CNS strategies for dealing with conflicting mechanical functions have also been described in other systems. For example, iguanas can run, but they need to stop to breathe. This occurs because they cannot "share" their intercostal muscles, which are required to act as prime movers in both tasks, and mechanically this is impossible (Carrier 1991). Similarly, cats combine paw shake with the swing phase of locomotion, but continue to walk during stance (Carter and Smith 1986). Trunk muscles in this study were never found to alternate back and forth between tasks or to drop out of one task to which they had previously contributed, suggesting that the tasks investigated in this study were mechanically compatible.

Nonlinear addition

Nonlinear addition implies that characteristics of each individual task are still evident, but that significant differences occur in amplitudes and/or timing. In both experiments there was always one holding muscle that showed nonlinear addition. One explanation may be that these nonlinear holding muscles were preferentially activated because they are the best choice to meet the mechanical demands of one task more than another. For example, in experiment 1, the UppAbd showed nonlinear addition. Previous studies have suggested that the upper abdominal muscles is specialized to produce trunk flexion (Abe et al. 1996; Carman et al. 1972; Oddsson and Thorstensson 1987; Strohl et al. 1981; Thorstensson et al. 1985) due to their more direct effects on the rib cage (Melissinos et al. 1981; Mier et al. 1985; Tesh et al. 1987). This was in contrast to lower abdominal muscles that appear more important for generation of abdominal pressure. Indeed, the external oblique muscle, which was most superficial to the UppAbd electrodes, has been shown not to exert force on the thoracolumbar fascia, the soft tissue structure involved in the generation of abdominal pressure (Tesh et al. 1987). Nonlinear addition may have occurred at the UppAbd region, therefore, because the external oblique was responding to moment-to-mo-

ment changes in the mechanical demands required to stabilize the rib cage.

Similarly, the muscles in the MedBack region in experiment 2 may have been preferentially activated for its function to stabilize the spine. The most superficial muscle in this region, the multifidus, originates from lumbar transverse processes and inserts on spinous processes only two to three segments superiorly. Hence it has been implicated as playing a large role as a sensor and responder to the small changes in intersegmental forces required to maintain spinal alignment (Crisco and Panjabi 1990; Donisch and Basmajian 1971). As further support of its specialized role, previous studies have shown that muscles in this region are maximally activated during isometric holding tasks and are minimally activated during movement as velocity is increased (Anderson et al. 1977; Jonsson 1970). In fact, for one subject of this study the MedBack (probably the multifidus) did not contribute to the pressure task but was tonically activated for all tasks of this study. Thus the findings indicate that for the MedBack region nonlinear addition may occur because of the specialized role of the multifidus for spinal stability. Muscles in the MedBack region may not be required to contribute to the generation of phasic pressure pulses, unlike muscles in the UppAbd region.

Whether a muscle shows preferential activation for one task more than another may change if its mechanical advantage is affected by task requirements associated with the combined task. For example, chest wall shape changes may have occurred and changed the mechanical relationships among trunk muscles, allowing other synergists to contribute more activity in the combined task. Thus during experiment 1 (holding in extension and pulsed expiratory efforts) the size of the rib cage may have increased as a result of abdominal muscle activation, displacing the abdomen inward and concomitantly raising intra-abdominal pressure (Melissinos et al. 1981; Mier et al. 1985). Thus an increased rib cage size may have lengthened other pressurizing muscles (e.g., internal intercostals, diaphragm), placing them at a better mechanical advantage for producing quick pressure pulses. Although not included in this study, measurements of chest wall shape using magnetometry would have provided direct evidence of chest wall shape change for the findings of nonlinear addition.

In summary, the findings of this study confirm the hypothesis that a linear addition of trunk muscle activity occurs when performance criteria are tightly controlled. It is not known whether subjects alter the performance of combined tasks during everyday life such that there is little need for linear addition. Regardless, the present study demonstrates that muscles can be shared for two different voluntary tasks without changing their contribution to either component task. As everyday tasks involve the simultaneous performance of voluntary breathing-related behaviors with various trunk movements, linear addition provides a relatively straightforward mechanism for combining breathing-related behaviors with

other trunk behaviors. On the other hand, a nonlinear addition allows for flexibility in the activation of specific muscles to take advantage of a muscle's particular mechanical effectiveness and to allow a movement to adapt to environmental constraints without having to reconfigure or construct a new plan.

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