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Greater Movement-Related Cortical Potential During Human Eccentric Versus Concentric Muscle Contractions

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Fang, Yin, Vlodek Siemionow, Vinod Sahgal, Fuqin Xiong, and Guang H. Yue. Greater movement-related cortical potential during human eccentric versus concentric muscle contractions. *J Neurophysiol* 86: 1764–1772, 2001. Despite abundant evidence that different nervous system control strategies may exist for human concentric and eccentric muscle contractions, no data are available to indicate that the brain signal differs for eccentric versus concentric muscle actions. The purpose of this study was to evaluate electroencephalography (EEG)-derived movement-related cortical potential (MRCP) and to determine whether the level of MRCP-measured cortical activation differs between the two types of muscle activities. Eight healthy subjects performed 50 voluntary eccentric and 50 voluntary concentric elbow flexor contractions against a load equal to 10% body weight. Surface EEG signals from four scalp locations overlying sensorimotor-related cortical areas in the frontal and parietal lobes were measured along with kinetic and kinematic information from the muscle and joint. MRCP was derived from the EEG signals of the eccentric and concentric muscle contractions. Although the elbow flexor muscle activation (EMG) was lower during eccentric than concentric actions, the amplitude of two major MRCP components—one related to movement planning and execution and the other associated with feedback signals from the peripheral systems—was significantly greater for eccentric than for concentric actions. The MRCP onset time for the eccentric task occurred earlier than that for the concentric task. The greater cortical signal for eccentric muscle actions suggests that the brain probably plans and programs eccentric movements differently from concentric muscle tasks.

INTRODUCTION

All motor actions involving skeletal muscle activities are accomplished by three types of muscle contractions: concentric (shortening), eccentric (lengthening), and isometric (constant length). Of the three, isometric and concentric contractions are more widely studied, and the neural mechanisms that mediate isometric and concentric actions are better understood. Eccentric muscle contractions, which generate a significant proportion of our daily-living movements [e.g., walking upstairs (concentric) and downstairs (eccentric); raising a water glass to the mouth (concentric) and returning it to the table (eccentric)], are less well understood.

Eccentric muscle actions are employed in many medical rehabilitation programs, such as those for anterior knee pain (Bennett and Stauber 1986), pitching shoulder injury (Pappas et al. 1985), and patellar tendinitis (Jensen and Fabio 1989). Numerous athletic training and recreational conditioning programs also include eccentric muscle activities as a major component of these programs (Alfredson et al. 1999; Bobbert 1990; Chandler et al. 1989; Wilk et al. 1993). A major advantage of eccentric muscle actions is that this type of muscle activity develops greater tension than concentric actions (Bigland and Lippold 1954; Doss and Karpovich 1965; Lacerte et al. 1992; Olson et al. 1972). In addition, eccentric training induces adaptive changes in the muscle, which may reduce future tissue damage and pain (Clarkson et al. 1992; Fridén et al. 1983a; Hortobágyi et al. 1996). Eccentric contractions require less energy expenditure, and such energy efficiency may improve the functional capacity of an individual with limited physiological reserves (Asmussen 1952; Bigland-Ritchie and Woods 1976; Dean 1988). Yet, little is known about how eccentric training or exercise affects the CNS.

The results of many studies suggest that the CNS may control concentric and eccentric muscle actions differently. One of the most reported observations is that for a given force to be generated, electromyographic (EMG) activities are lower during eccentric than concentric contractions (e.g., Bigland and Lippold 1954; Moritani et al. 1988; Tesch et al. 1990). A lower level of EMG in an eccentric contraction is a result of fewer motor units being recruited and a lower discharge rate of the active motor units (Moritani et al. 1988). Nardone et al. (1989) reported that motor unit recruitment order during eccentric contractions of human triceps surae muscles was reversed compared with isometric and concentric contractions. High-threshold motor units were selectively recruited (Howell et al. 1995; Karapondo et al. 1993; Nardone et al. 1989), and the activation was shifted from a slow (soleus) to a fast (gastrocnemius) muscle when an eccentric contraction was performed (Nardone and Schieppati 1988). One interesting observation is that the motor unit pool of a muscle cannot be fully activated during maximal voluntary eccentric contractions, as assessed by the twitch interpolation technique, whereas almost all motor units are active during concentric contractions (Sale 1988; Westing et al. 1990). The amplitude of motor-evoked potential in muscle by transcranial magnetic stimulation differs for con-

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centric and eccentric contractions. With comparable EMG levels, the motor-evoked potential in an elbow flexor muscle was less for eccentric contractions than for concentric and isometric contractions (Abbruzzese et al. 1994). Relative activation levels among synergistic muscles change as the activity shifts from concentric to eccentric muscle actions (Nakazawa et al. 1993).

Despite these differences, which have led a number of investigators to suggest that eccentric muscle actions have unique neural control strategies (Enoka 1996), no direct evidence is available to indicate that the CNS signal for controlling an eccentric muscle contraction differs from that for controlling a concentric action. The purpose of this study was to measure electroencephalography (EEG)-derived movement-related cortical potential (MRCP) during the two types of muscle actions and determine if the level and timing of cortical activation differ between eccentric and concentric human elbow flexor contractions. Preliminary results have been reported in abstract form (Siemionow et al. 1999).

METHODS

Subject

Eight right-handed volunteers (6 men and 2 women, 27.75 ± 7.21 yr old, range 20–44 yr) participated in the study. All individuals were healthy and had no known neuromuscular disorders. All individuals gave informed consent prior to their participation. The experimental procedures were approved by the Institutional Review Board at the Cleveland Clinic Foundation.

Mechanical recording

Subjects were seated comfortably in an experimental chair in an electrically shielded data-recording room. The subject's left arm was held at shoulder height, then placed and restrained on a wooden board that could be freely rotated. The forearm was in a neutral position between supination and pronation. The upper arm rotated ~30° forward from a straight line connecting the left and right shoulders. The subject's torso, shoulders, and left upper arm were all stabilized so that only movements at the left elbow joint were allowed (Fig. 1). A load of 10% of the subject's body weight was attached to the left wrist through a nonelastic cable and a pulley fixed on the wall (Fig. 1). Subjects could perform concentric contraction of the elbow flexor muscles by lifting the weight and eccentric contraction by lowering the weight. The wooden board on which the arm rested was connected to a potentiometer that measured the position of the arm and the angle of the elbow joint. A concentric or eccentric contraction consisted of a 30° rotation of the elbow joint. A trigger signal was generated as soon as the rotation reached a threshold (3°). This trigger signal was later used for the triggered data averaging during data processing and analysis. A button-type strain gauge force transducer (subminiature load cell, Sensotec, Columbus, OH) was built between two metal plates; one was attached to one side of the cable holding the weight and the other to the opposite side of the cable fixed to the subject's arm. When the weight was lifted or lowered, the transducer was pressed and force recorded. The position and force signals were digitized (100 samples/s) by a Spike 2 data acquisition and analysis system (Cambridge Electronic Design Limited, Cambridge, UK) and recorded on-line on the hard drive of a personal computer. The position and force signals were displayed on an oscilloscope located in front of the subject.

Electrical recording

EEG RECORDING. Monopolar EEG data were recorded from four locations using Ag-AgCl cup electrodes (10-mm diam). Positioning of the electrodes was based on the International 10–20 System (Jasper 1958). One electrode (Cz) was placed on the scalp overlying the supplementary motor area (SMA). Another (Fz) was over the center region of the prefrontal cortex. C3 and C4 electrodes were positioned on the scalp overlying the sensorimotor areas of the left and right hemispheres, respectively. These four active electrodes (Cz, C3, C4, and Fz) were referenced to the common linked earlobes (A1 and A2). Impedance of each electrode was maintained 5000 Ω. The EEG signal was amplified (20,000 times) using EEG amplifiers (Grass Neurodata Amplifier System, Astro-Med, West Warwick, RI). The time constant of the EEG recording was 2s, with a low-pass cutoff frequency of 100 Hz. The output signal from the EEG amplifiers was digitized (200 samples/s) using the Spike 2 system and recorded on the hard disk of the personal computer.

EMG RECORDING. Surface EMG signals were simultaneously recorded from the biceps brachii (BB), brachioradialis (BR), triceps brachii (TB), and deltoid (DL) muscles. The skin was cleaned with alcohol prior to electrode attachment. Bipolar electrodes (8-mm recording diameter) were attached to the skin overlying the belly of each muscle. The reference electrode was fixed on the skin overlying the lateral epicondyle near the elbow joint. The EMG signals were amplified (1,000 times), filtered (10–3,000 Hz), digitized (1,000 samples/s), and recorded on the hard disk of the computer.

Experimental procedures

After the scalp was cleaned with alcohol pads, EEG electrodes were attached to the scalp with electrode paste. The impedance of each electrode was measured after the electrodes were secured on the scalp. If the impedance for a given electrode was >5,000 Ω, the electrode was removed and the scalp was further prepared until the impedance was lowered to <5,000 Ω. The left elbow and forearm rested on the padded wooden board after the EMG electrodes were attached. The forearm was secured between two vertical wooden boards that could

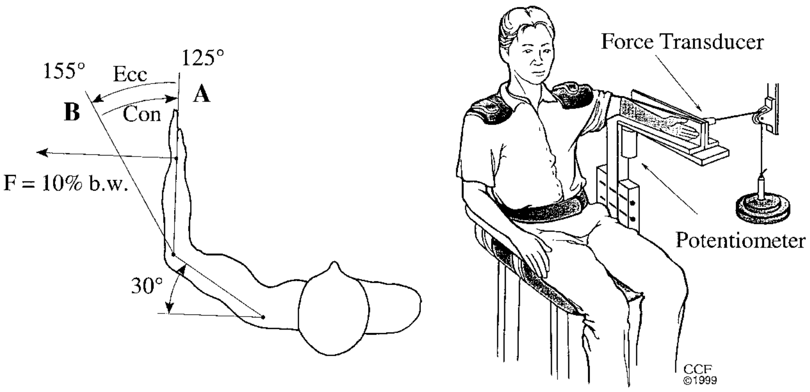

FIG. 1. Illustration of the experimental setup. *Left*: a top view of the angle and range of movements.

be tightly screwed onto the horizontal board (Fig. 1, *right*). Soft cushions were provided between the forearm and vertical boards.

Each subject performed 50 concentric and 50 eccentric contractions of the elbow flexor muscles of the left arm. Four subjects performed the concentric contractions first, and the other four performed the eccentric trials first. Subjects rested for 5 min after the first 50 contractions were completed. During this time, they were released from the chair and arm restraints, but with the EEG and EMG electrodes still attached, to allow them to stretch. During each concentric contraction, the elbow flexors shortened and the elbow joint rotated from the 155° position to the 125° position (180° with the elbow being fully extended). During each eccentric contraction, the muscles lengthened and the elbow joint rotated from the 125° position to the 155° position (Fig. 1, *left*). Both the beginning arm position (155° for concentric and 125° for eccentric) and target position (125° for concentric and 155° for eccentric) were displayed on an oscilloscope. The subject moved the forearm (rotated the elbow) from the beginning position to the target position and the weight was either caught by the experimenter (concentric) or touched down on the padded floor (eccentric) after the target position was passed. After each contraction, the experimenter supported the weight (concentric) or the weight was on the floor (eccentric) for ∼10 s, during which the subject rested. After the rest, the weight and subject's arm were moved back to the beginning position by the experimenter and the subject began the isometric contraction (∼5 s) that preceded each concentric or eccentric movement. The speed of movement was ∼25°/s for both actions.

Subjects gauged the range and speed of each movement by viewing the position cursor on the oscilloscope. They were told to avoid eye blinks during each contraction, but eye blinks were allowed during the time when the weight was supported by the experimenter. At the end of the experiment, maximal isometric elbow flexion, extension and shoulder abduction contractions were performed to record maximal EMG values of the BB, BR, TB, and DL muscles. These maximal EMG values were later used to normalize the EMG data of these muscles during the concentric and eccentric contractions.

Analysis

All raw EEG data were inspected visually. Trials that contained eye blinks or other signal artifacts were excluded. For both concentric and eccentric contractions, each trigger signal triggered a 10-s window (5 s before the trigger and 5 s after). The Spike 2 data analysis software performed EEG signal averaging over the 50 trials of each type of contractions. Similarly, after all EMG signals were rectified, the force and EMG signals were trigger-averaged across the 50 trials. After averaging, the baseline force, EMG, and EEG data were measured. Baseline data were defined as the data obtained during the isometric contraction (the holding phase). During the concentric and eccentric contractions, mean force and EMG were determined within 1.2 s from the time of trigger. Force fluctuation (standard deviation of the mean force) was measured for the first five and last five trials of concentric and the first five and last five trials of eccentric contractions. In each trial, it was calculated in a period during the movement when the force was stable (Fig. 2*A*). In each subject, the fluctuation was measured from each of the 10 trials first, then an average of the 10 trials was obtained.

MRCP was divided into two major components, negative potential (NP) and positive potential (PP). These components were measured separately. In general, NP is thought to be related to movement preparation, planning, and execution, whereas PP is associated with brain signals processing feedback information from the sensory system (Deecke et al. 1976; Hallet 1994; Siemionow et al. 2000). Mean and peak values were determined for the NP. The mean NP was calculated as an average from the beginning of NP to its peak, and the peak NP was determined from the baseline to the peak (Fig. 2*B*). In addition, the onset time of NP was analyzed to reveal possible differences in the timing of the NP between the two motor tasks. The NP onset time was calculated from the trigger to the beginning of NP and from the onset of the biceps brachii EMG to the onset of NP. The beginning of the NP was determined by a curve-fitting procedure—a straight line was drawn along the baseline potential and another line along the NP. The intercept of the baseline and the line crossing NP was taken as the beginning of the NP (Siemiomow et al. 2000).

Three amplitude values were measured for PP. The mean PP was the mean value from the negative peak or beginning of the PP to the end of movement (based on elbow angle measurement). The peak PP was the amplitude from the beginning of PP to the value at which the movement was ended. The baseline PP was measured from the pre-NP baseline to the value at which the movement was ended (Fig. 2*B*). These measurements were averaged across all subjects. Finally, the range and speed of movement for each type of contractions were measured.

Statistical analysis

Paired *t*-tests were performed to compare force, EMG, range and rate of movement, and measurements of MRCP between the concentric and eccentric muscle contractions. The mean force, EMG, and

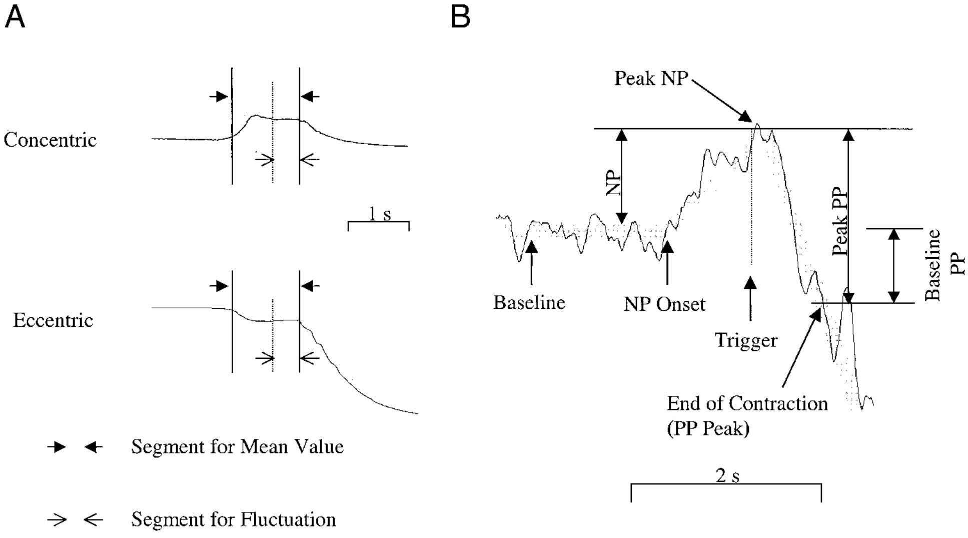

FIG. 2. *A*: illustrations of mean force and force fluctuation measurements for concentric and eccentric actions. The mean force was an average between the trigger and end of movement (between the filled arrows). Force fluctuation was measured from a period when the force was stable (between the open arrows). *B*: components of movement-related cortical potential (MRCP) and illustrations of their measurements. NP, negative potential; PP, positive potential. Mean NP was an average from the baseline to the peak of NP, and peak NP was the amplitude from the baseline to the peak value of the NP. Mean PP was an average from the peak NP to PP peak, Peak PP was the amplitude from the peak NP to the PP peak, and baseline PP was the amplitude from the baseline to the PP peak. The NP onset time was from the trigger (dotted vertical line) to the NP onset. Another NP onset time was measured from the EMG onset (not shown) to the NP onset.

EEG values during the baseline condition were also compared between the two types of contractions using the paired *t*-tests. Significance level was determined at $P \leq 0.05$, and the data are reported as means ± SD unless otherwise mentioned.

RESULTS

Initial isometric contraction

Subjects held the weight for ~5 s (isometric contraction) before each eccentric or concentric contraction. The mean isometric force preceding the eccentric contraction (60.17 ± 7.98 N) was not significantly different ($P > 0.15$) from that preceding the concentric contraction (63.89 ± 8.68 N, Fig. 3*A*). Surface EMG data recorded from the BB, BR, TB, and DL muscles during the isometric contraction that preceded the concentric and eccentric contractions were similar ($P > 0.3$, Fig. 3*B*). The isometric EMG data (percent of MVC) of the BB, BR, TB, and DL muscles before the eccentric contraction were 27.68 ± 4.68, 26.83 ± 6.49, 7.10 ± 0.86, and 7.01 ± 0.23%, respectively. The same values for the four muscles before the concentric contraction were 26.56 ± 6.38, 24.47 ± 6.60, 6.98 ± 0.84, and 7.21 ± 0.34%, respectively (Fig. 3*B*). Similarly, the mean EEG amplitude during the isometric contraction preceding the eccentric contraction did not significantly differ ($P > 0.2$) from that preceding the concentric contraction (Fig. 3*C*). The isometric EEG values for the four scalp locations (Cz, C3, C4, and Fz) before the eccentric contraction were −0.72 ± 0.26, −0.13 ± 0.09, −0.50 ± 0.37, and −0.18 ± 0.09 μV, respectively. The isometric EEG values for the four recording locations before the concentric contraction were −0.64 ± 0.25, −0.12 ± 0.07, −0.52 ± 0.31, and −0.15 ± 0.08 μV, respectively (Fig. 3*C*).

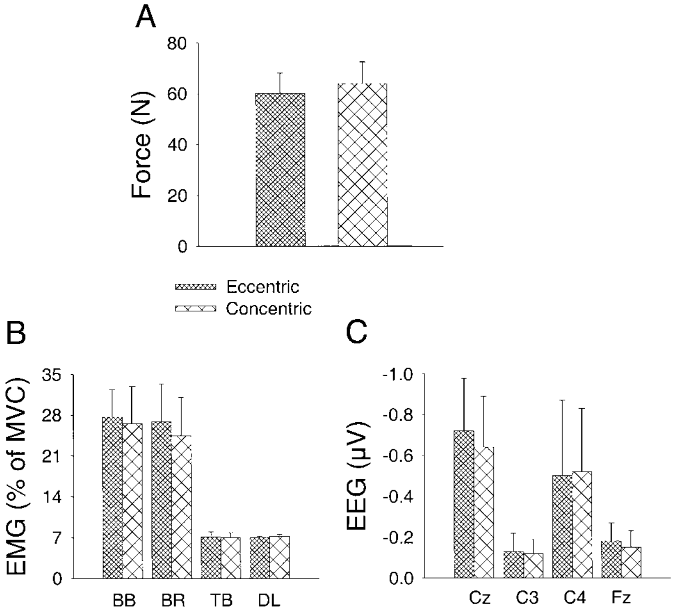

FIG. 3. Force (*A*), electromyography (EMG; *B*), and average electroencephalography (EEG; *C*) during the isometric contraction (holding phase) that preceded each eccentric and concentric contraction of the elbow flexor muscles. All values during the holding phase before the eccentric task were similar to the same measurements preceding the concentric action. BB, biceps brachii; BR, brachioradialis; TB, triceps brachii; DL, deltoid muscle. Cz, C3, C4, and Fz are electrode positions overlying the supplementary motor area, left hemisphere sensorimotor cortex, right hemisphere sensorimotor cortex, and central prefrontal cortex, respectively.

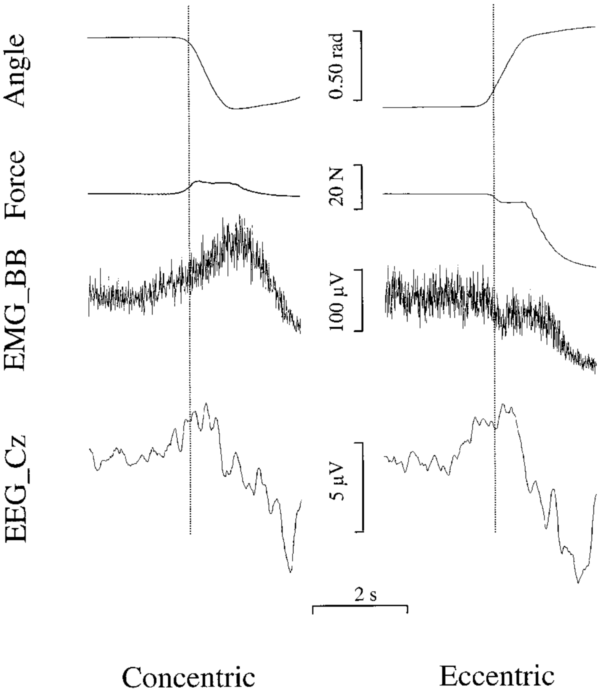

FIG. 4. Examples of joint angle, force, EMG (biceps brachii), and MRCP (Cz electrode) for concentric (*left*) and eccentric (*right*) contractions of a subject. Vertical dotted lines indicate the timing of trigger. Note that although the load supported by the subject was the same between the 2 tasks, the force increased during concentric and decreased during eccentric contractions from the baseline (isometric) force. The differential changes in force were due to different cable-pulley friction forces between the eccentric and concentric conditions (see METHODS).

Eccentric and concentric contractions

RANGE AND SPEED OF MOVEMENT. The range of movement for eccentric and concentric contractions was the same: 0.49 ± 0.09 and 0.49 ± 0.05 rad, respectively. The speed of movement for the eccentric contraction (0.40 ± 0.02 rad/s) was not significantly different ($P > 0.1$) from that for the concentric contraction (0.37 ± 0.03 rad/s). Figure 4 (*top*) presents an example of movement range and speed for concentric (*left*) and eccentric (*right*) contractions.

FORCE AND EMG. Although the load (weight) applied during eccentric and concentric contractions was the same, the force exerted by the subjects during eccentric contractions (54.50 ± 6.03 N) was significantly lower ($P < 0.01$) than the force during concentric contractions (69.33 ± 8.30 N, Figs. 4, *2nd panel,* and 5*A*). We recently moved the force transducer to the distal side of the pulley (between the pulley and weight) and found that the force was the same during eccentric and concentric contractions against the same weight. Thus the discrepancy in force under the same-load conditions arose from different friction force directions between the cable and pulley when the weight was lowered and lifted. If the friction force was the same, then the exerted force should also be equal between the two tasks.

The EMG of the two elbow flexor muscles during eccentric contractions (20.04 ± 2.46% for BB and 18.61 ± 4.18% for BR) was significantly lower ($P < 0.01$) than the EMG of the two muscles during the concentric contractions (40.55 ± 8.27% for BB and 48.20 ± 11.45% for BR, Figs. 4, *3rd panel,* and 5*B*). Note that the EMG of the BB and BR muscles for the

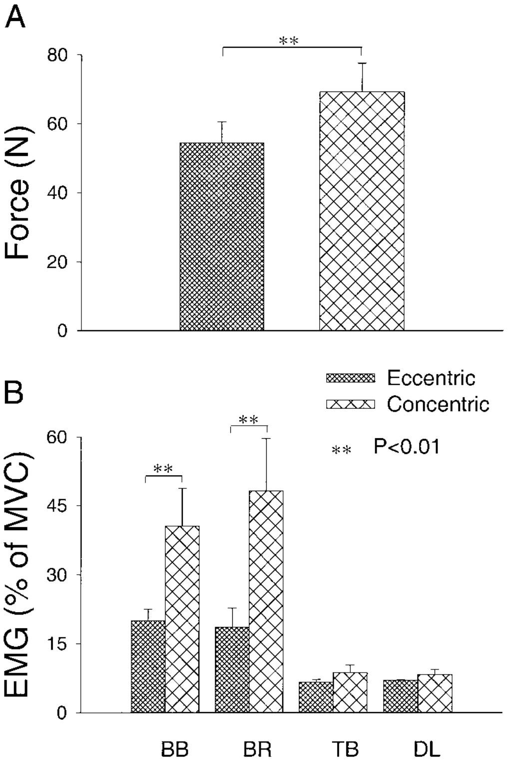

FIG. 5. Force (*A*) and EMG (*B*) measured during eccentric and concentric contractions of the elbow flexor muscles. Both the force and EMG of the elbow flexor muscles (BB and BR) during the eccentric action were significantly lower than the values during the concentric task.

concentric contraction was more than double that of the EMG for the eccentric contraction. The EMG levels of these two muscles during the eccentric contraction were slightly lower than those during the isometric contraction (compare Figs. 3*B* and 5*B*). However, the EMG data for the TB (6.60 ± 0.62% for eccentric and 8.66 ± 1.69% for concentric) and DL (6.98 ± 0.23% for eccentric and 8.24 ± 1.18% for concentric) muscles were similar ($P > 0.05$, Fig. 5*B*).

MRCP NEGATIVE POTENTIAL. Mean and peak values of the NP were measured. For the eccentric contraction, the mean NP values for the four scalp locations (Cz, C3, C4, and Fz) were −1.60 ± 0.40, −0.85 ± 0.14, −1.41 ± 0.51, and −0.86 ± 0.28 μV, respectively. For the concentric contraction, these four values were −1.04 ± 0.31, −0.56 ± 0.15, −1.00 ± 0.48, and −0.48 ± 0.31 μV, respectively (Figs. 4, *bottom*, and 6*A*). The mean NP values for the eccentric contraction were significantly greater than those for the concentric contraction (Cz, $P < 0.05$; C3, $P < 0.005$; C4, $P < 0.02$; and Fz, $P < 0.005$). For the eccentric contraction, the peak NP values for the four recording locations (Cz, C3, C4, and Fz) were −3.78 ± 0.74, −2.68 ± 0.22, −3.41 ± 0.59, and −3.21 ± 0.45 μV, respectively. The corresponding four values for the concentric contraction were −2.80 ± 1.19, −2.02 ± 0.58, −2.76 ± 0.90, and −2.48 ± 0.71 μV, respectively (Figs. 4, *bottom*, and 6*B*). The peak NP values for the eccentric contraction were significantly greater than those for the concentric contraction (Cz, $P < 0.05$; C3, $P < 0.02$; C4, $P = 0.05$; and Fz, $P < 0.002$).

NP ONSET TIME. The NP onset time was measured from the trigger to the beginning of NP. The values of NP onset time for the eccentric task for the four recording locations (Cz, C3, C4, and Fz) were −859 ± 48, −837 ± 58, −890 ± 89, and −842 ± 52 ms, respectively. For the concentric task, the four values were −768 ± 62, −681 ± 83, −802 ± 43, and −758 ± 38 ms, respectively (Fig. 7*A*). The values of NP onset time for the eccentric contraction were significantly longer than those for the concentric contraction (Cz, $P < 0.05$; C3, $P < 0.05$; C4, $P < 0.05$; and Fz, $P < 0.05$). The NP onset time was also measured from the onset of NP to the onset of the biceps brachii EMG. This value allowed us to determine the latency from the beginning of the cortical activity to the onset of muscle activation. For the eccentric task, the values of NP onset time from the EMG activity for the four recording locations (Cz, C3, C4, and Fz) were −546 ± 40, −535 ± 26, −538 ± 55, and −595 ± 30 ms, respectively. For the concentric task, the four values were −458 ± 34, −430 ± 23, −451 ± 19, and −528 ± 25 ms, respectively (Fig. 7*B*). The onset time values for the eccentric contraction were significantly longer than those for the concentric contraction (Cz, $P < 0.05$; C3, $P < 0.05$; C4, $P < 0.05$; and Fz, $P < 0.05$).

MRCP POSITIVE POTENTIAL. For the eccentric contraction, the mean PP values for the four recording locations (Cz, C3, C4, and Fz) were 0.84 ± 0.51, 1.45 ± 0.63, 0.77 ± 0.16, and 0.99 ± 0.39 μV, respectively. For the concentric contraction, the four values were 0.18 ± 0.07, 0.78 ± 0.17, 0.18 ± 0.09, and 0.09 ± 0.13 μV, respectively (Fig. 8*A*). The mean PP values for the eccentric contraction were significantly greater than those for the concentric contraction (Cz, $P < 0.05$; C3, $P < 0.02$; C4, $P < 0.005$; and Fz, $P < 0.001$). The peak PP values for the eccentric contraction at the four scalp locations were 6.06 ± 0.40, 6.13 ± 0.74, 6.38 ± 1.33, and 8.37 ± 3.45 μV, respectively. These four values for the concentric task

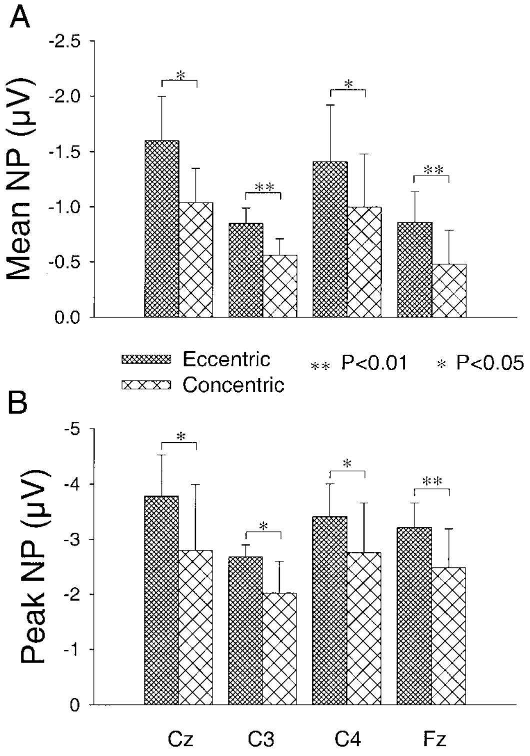

FIG. 6 Mean (*A*) and peak (*B*) NP of MRCP measured during eccentric and concentric contractions. Both the mean and peak NP values were greater for eccentric than concentric actions at all 4 recording locations.

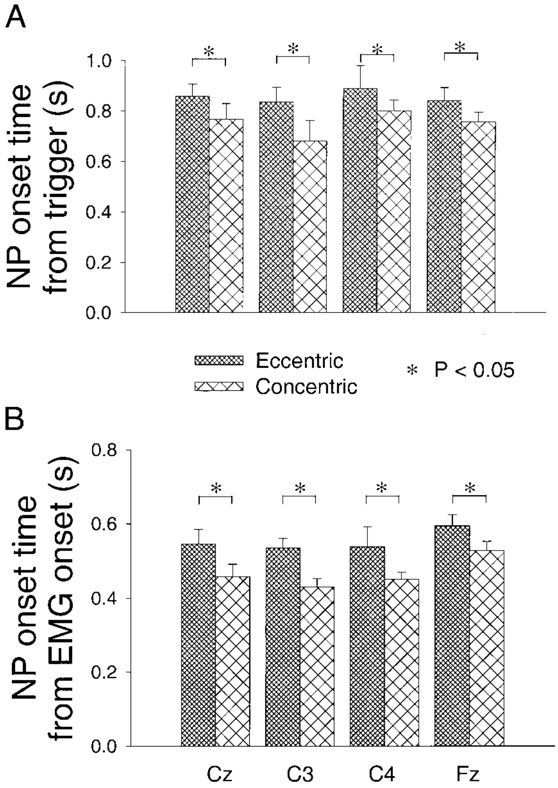

FIG. 7. NP onset time for the eccentric and concentric tasks. The onset time was measured from onset of the trigger to the beginning of the NP (*A*) and from onset of the BB EMG to the beginning of the NP (*B*). Both measurements of the onset time were significantly longer for eccentric than concentric actions.

were 4.74 ± 0.66, 4.41 ± 0.83, 3.89 ± 1.60, and 5.11 ± 1.62 μV, respectively (Fig. 8*B*). Three of the four peak PP values for the eccentric task were significantly greater than those for the concentric task (Cz, $P < 0.05$; C3, $P < 0.05$; C4, $P < 0.05$; and Fz, $P = 0.08$). The baseline PP values for the eccentric task at the four scalp locations were 2.29 ± 0.88, 3.46 ± 0.65, 2.97 ± 1.67, and 5.17 ± 3.39 μV, respectively. The four values for the concentric action were 1.94 ± 1.76, 2.39 ± 1.23, 1.13 ± 1.65, and 2.64 ± 1.72 μV, respectively (Fig. 8*C*). Two of the four baseline PP values for the eccentric task were significantly greater than those for the concentric task (Cz, $P = 0.6$; C3, $P < 0.05$; C4, $P = 0.06$; and Fz, $P < 0.05$).

FORCE FLUCTUATION. The force fluctuation (SD) was 1.14 ± 0.61 N for the eccentric task and 0.76 ± 0.25 N for the concentric task. The two values were significantly different ($P < 0.05$).

DISCUSSION

The purpose of this study was to determine whether EEG-measured brain activity associated with eccentric contractions of the elbow flexor muscles differs from that related to concentric contractions. The major findings were that MRCP NP values, which are related to cortical activities for movement preparation and execution, were greater during eccentric than concentric tasks; MRCP PP values, which are associated with the processing of feedback signals, were greater during eccentric than concentric actions; and the onset times of the NP were earlier for the eccentric than concentric muscle contractions.

EEG (MRCP) and EMG paradox

For the eccentric task, the MRCP NP measurements were greater but the EMG and force of the elbow flexor muscles were lower than the corresponding values of the concentric task (lower MRCP but higher EMG and force). These observations are contradictory to current data dealing with the relationship between cortical and muscle signals. In monkey, a higher discharge rate of motor cortical neurons was associated with greater exerted force (Cheney and Fetz 1980; Evarts 1968; Hepp-Reymond et al. 1989; Smith et al. 1975). A number of studies have shown a positive relationship between MRCP NP and muscle output in human subjects (Becker and Kristeva 1980; Kutas and Donchin 1974; Shibata et al. 1993). A recent study from this laboratory (Siemionow et al. 2000) reported a linear relationship between a major component of MRCP NP (negative slope) recorded from scalp locations overlying the sensorimotor and supplementary motor areas and human elbow flexion force and elbow flexor muscle EMG. Based on these relationship data, given greater MRCP NP for the eccentric action, we should expect *higher* force and EMG for the eccentric contraction. This expectation is based on the assumption that the NP is a measure of the signal of the motor cortical output neurons that scales muscle output.

However, it is unlikely that the NP is related only to the cortical output signals. The NP onset time was >400 ms before onset of EMG activity for both the eccentric and concentric actions, during which early preparation and planning for the muscle action should also occur. The following section discusses possible explanations for greater NP that may be related to differential cortical programming/planning for an eccentric muscle contraction.

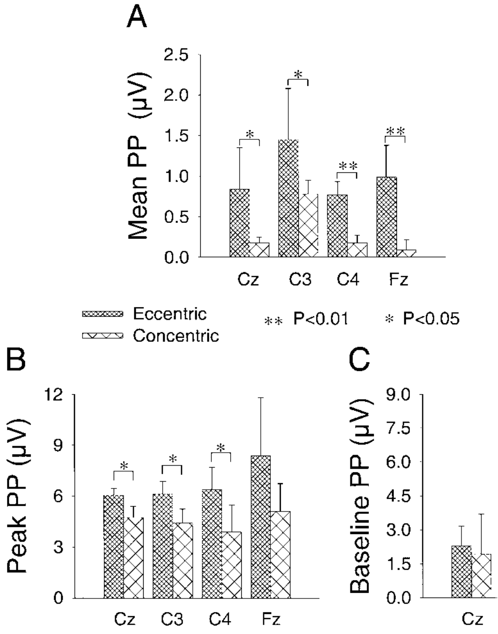

FIG. 8. Mean (*A*), peak (*B*), and baseline (*C*) PP of MRCP for the eccentric and concentric actions. Both the mean and peak PP values were significantly greater for eccentric than concentric tasks at all recording locations except the peak PP at Fz location ($P = 0.07$). Two of the 4 locations (C3 and Fz; for C4, $P = 0.057$) showed significantly greater baseline PP during eccentric than concentric actions.

Possible explanations for greater MRCP NP during eccentric muscle actions

DEGREE OF DIFFICULTY. Eccentric contractions are more difficult to perform than concentric ones. This is supported by the result of higher eccentric than concentric force fluctuations. Higher eccentric force fluctuation seems consistent with the observation that high-threshold motor units are selectively recruited and that they discharge action potentials at a lower rate during submaximal eccentric contractions (Howell et al. 1995; Nardone et al. 1989). Because high-threshold motor units exhibit greater twitch force and a lower discharge rate makes less-complete fused motor unit force, it is not surprising that force fluctuation is higher during eccentric than concentric contractions. Owings and Grabiner (2000) reported greater errors (force fluctuation) in controlling eccentric than concentric knee extensor contractions. To control a movement with a higher degree of difficulty, the brain may need to devote greater effort or a more extensive neural network may be needed to participate in the controlling process. Neuroimaging studies have shown that when motor tasks with a higher degree of difficulty are performed, the level of brain activation is higher (Roland et al. 1980; Yue et al. 2000).

PREVENTING MUSCLE DAMAGE. Eccentric muscle contractions are characterized by greater tissue damage as compared with concentric ones (Newham et al. 1983; Shellock et al. 1991; Waterman-Storer 1991). Histological and ultrastructural muscle damage has been reported after eccentric exercise, including sarcolemmal disruption, dilation of the transverse tubule system, distortion of myofibrillar components, fragmentation of the sarcoplasmic reticulum, lesions of the plasma membrane, cytoskeletal damage, and changes in the extracellular myofiber matrix (Fridén and Lieber 1992; Fridén et al. 1983b; Stauber 1989). Because of higher susceptibility of tissue to damage from eccentric contractions, the CNS may need to plan ahead to modify the descending command to limit the damage. The additional planning activity in the cortex for the "damage reduction" may contribute to the greater NP signal.

One particular plan for the damage reduction by the CNS might be concurrent modulation (gating by presynaptic input) of the Ia afferent input from the lengthening muscle, to attenuate elicitation of the unwanted stretch reflex at the spinal cord level. This speculation is supported by the finding that monosynaptic reflex excitability is depressed during eccentric contractions of both upper (Abbruzzese et al. 1994) and lower (Romano and Schieppati 1987) limb muscles. If the reflex excitability is not depressed, muscle force during eccentric contractions would further increase, which could lead to more muscle damage.

DIFFERENT CONTROL STRATEGY. It has been reported that the motor unit recruitment pattern differs from eccentric to concentric contractions (Hoffer et al. 1980; Moritani et al. 1988; Schieppati et al. 1987). During an eccentric contraction, high-threshold motor units are selectively recruited as compared with a concentric or isometric contraction, in which low-threshold motor units are recruited first (Howell et al. 1995; Nardone et al. 1989). An altered motor unit recruitment order may reflect a unique nervous system control strategy for eccentric actions, and that strategy may need greater cortical activity to carry it out. However, a recent study (Bawa and Jones 1999) suggested that selective recruitment of high-threshold motor units does not occur during eccentric contractions of human wrist flexor muscles. More studies are needed to determine whether a reversal in motor unit recruitment order is a robust phenomenon for eccentric muscle actions.

Influence of speed of movement on MRCP NP

It is expected that the amplitude of MRCP NP depends on the rate or speed of the movement because greater muscle (and presumably brain) activities are needed to move the same load at a faster speed (force-velocity relationship). In the present study, the speed of movement was the same during eccentric versus concentric contractions. Thus the greater NP for the eccentric task in the present study did not have a biased contribution from the speed of movement.

MRCP PP

The MRCP PP was greater for the eccentric than concentric contractions. The PP was defined as the amplitude from the peak of the NP and the baseline to the value corresponding to the time of movement completion (right before the weight touched the floor). Because the peak of the NP occurred ~350 ms after the onset of EMG and the entire duration of PP was after this peak, this signal (PP) has little relation to movement planning and execution but must be more closely associated with feedback signals (e.g., sensory information from muscles and joints) to be processed in the brain (Hallett 1994; Kornhuber and Deecke 1965; Shibasaki et al. 1980; Tarkka and Hallett 1991). As indicated by force fluctuation data, eccentric movement is associated with higher force variability, which indicates that the movement is more difficult to control. Consequently, a greater amount of sensory information related to more variable eccentric actions may be conveyed to the brain. The higher level of PP may be a result of processing the eccentric-related sensory information. One source of sensory information that is likely to be greater during an eccentric (lengthening) than a concentric (shortening) muscle contraction is Ia afferent activity, which results from stretching muscle spindle receptors.

Experimental evidence has supported the view that the human stretch reflex has a delayed "long latency" response that is a transcortical reflex (e.g., Matthews 1991; Thilmann et al. 1991; however, see Corden et al. 2000). The notion of transcortical reflex implies that the stretch-induced Ia afferent volley causes firing of cortical neurons that, in turn, activate the muscle being stretched. It is very likely that this reflex-related cortical activity contributes to the PP because it occurs after the movement begins. On the contrary, there should be no stretch reflex-related cortical activity during a concentric muscle action because the muscle is not stretched.

Onset of NP

On average, the onset of NP for the eccentric task was ~100 ms earlier than that for the concentric contraction. The earlier NP onset time suggests that the brain began preparing for eccentric movement earlier than for the concentric task. The earlier onset time may be explained by additional cortical planning for more movement complexity, modulation of monosynaptic reflex excitability, and carrying out a different control (e.g., motor unit recruitment) strategy for an eccentric action.

Conclusions

It has long been speculated that the nervous system poses unique strategies for controlling eccentric muscle actions. This study shows, for the first time, that the brain plans eccentric movements and processes eccentric-related sensory information differently than it does for concentric muscle contractions. Because eccentric movements are more complex, make muscles more prone to damage, and perhaps require a unique motor unit recruitment strategy to carry out the actions, the greater NP may reflect additional cortical planning activities or effort to deal with these "special problems." The higher magnitude of MRCP PP for the eccentric contractions may indicate that a larger amount of sensory information is being processed in the brain and additional reflex-induced cortical activity resulted from stretching the muscles. The earlier NP onset time suggests that not only are the cortical activities associated with planning eccentric actions greater but also the neurons begin the planning activities earlier.

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