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Neural Control of Rhythmic Human Arm Movement: Phase Dependence and Task Modulation of Hoffmann Reflexes in Forearm Muscles

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Zehr, E. Paul, David F. Collins, Alain Frigon, and Nienke Hoogenboom. Neural control of rhythmic human arm movement: phase dependence and task modulation of Hoffmann reflexes in forearm muscles. *J Neurophysiol* 89: 12–21, 2003. 10.1152/jn.00416.2002. Although we move our arms rhythmically during walking, running, and swimming, we know little about the neural control of such movements. Our working hypothesis is that neural mechanisms controlling rhythmic movements are similar in the human lumbar and cervical spinal cord. Thus reflex modulation during rhythmic arm movement should be similar to that seen during leg movement. Our main experimental hypotheses were that the amplitude of H-reflexes in the forearm muscles would be modulated during arm movement (i.e., phase-dependent) and would be inhibited during cycling compared with static contraction (i.e., task-dependent). Furthermore, to determine the locus of any modulation, we tested the effect that active and passive movement of the ipsilateral (relative to stimulated arm) and contralateral arm had on H-reflex amplitude. Subjects performed rhythmic arm cycling on a custom-made hydraulic ergometer in which the two arms could be constrained to move together (180° out of phase) or could rotate independently. Position of the stimulated limb in the movement cycle is described with respect to the clock face. H-reflexes were evoked at 12, 3, 6, and 9 o'clock positions during static contraction as well as during rhythmic arm movements. Reflex amplitudes were compared between tasks at equal M wave amplitudes and similar levels of electromyographic (EMG) activity in the target muscle. Surface EMG recordings were obtained bilaterally from flexor carpi radialis as well as from other muscles controlling the wrist, elbow, and shoulder. Compared with reflexes evoked during static contractions, movement of the stimulated limb attenuated H-reflexes by 50.8% ($P < 0.005$), 65.3% ($P < 0.001$), and 52.6% ($P < 0.001$) for bilateral, active ipsilateral, and passive ipsilateral movements, respectively. In contrast, movement of the contralateral limb did not significantly alter H-reflex amplitude. H-reflexes were also modulated by limb position ($P < 0.005$). Thus task- and phase-dependent modulation were observed in the arm as previously demonstrated in the leg. The data support the hypothesis that neural mechanisms regulating reflex pathways in the moving limb are similar in the human upper and lower limbs. However, the inhibition of H-reflex amplitude induced by contralateral leg movement is absent in the arms. This may reflect the greater extent to which the arms can be used independently.

INTRODUCTION

We routinely perform rhythmic movements with the arms and legs during locomotor activities such as walking, running, swimming, and cycling. Numerous studies have revealed phasic patterns of muscle activity and reflex control associated with these forms of locomotion (Brooke et al. 1997; Schieppati 1987; Stein and Capaday 1988; Zehr and Stein 1999b). Many researchers have been interested in documenting the pattern of reflex control in these movements as a window into the neural control mechanisms on which the behaviors are predicated (Brooke et al. 1997). A particularly rich vein of study has been that of Hoffmann (H-) reflex modulation during walking and leg cycling. In a systematic set of experiments, Brooke and his colleagues evaluated the pattern of H-reflex modulation during leg cycling movement (Brooke et al. 1997). A distinct pattern of H-reflex attenuation (compared with control reflexes evoked while stationary) was observed during active (Brooke et al. 1992) and passive (McIlroy et al. 1992) movement of the stimulated leg as well as by active (McIlroy et al. 1992) and passive movement of the contralateral leg (Collins et al. 1993). Thus H-reflexes in the leg are modulated by motor task (i.e., task-dependent during rhythmic leg movement). The neural control mechanisms and patterns of reflex modulation during rhythmic arm cycling movements are not as well known.

Cutaneous reflexes have also been studied during human leg cycling (Brooke et al. 1999; Brown and Kukulka 1993; Zehr et al. 2001b). During active leg movement, cutaneous reflexes are modulated with position in the movement cycle (i.e., phase-dependent) (Brown and Kukulka 1993). This phase dependency is absent during passive movement (Brooke et al. 1999). The pattern of cutaneous reflex modulation evoked by stimulation of the superficial radial nerve at the wrist (Zehr and Chua 2000) during rhythmic arm cycling movement shared some

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features with the pattern of reflex modulation during leg movement seen after stimulation of the comparable nerve in the lower limb, the superficial peroneal nerve (Zehr et al. 1997). The amplitude of cutaneous reflexes in some muscles was linearly related to the ongoing background movement-related electromyography (EMG) (Zehr and Chua 2000). Other muscles such as posterior deltoid, biceps brachii, and flexor carpi ulnaris showed phase-dependent modulation such as seen in the lower limb (Zehr and Chua 2000). Stimulation of all three major cutaneous nerves innervating the hand during both arm cycling and static contraction showed that the overall pattern emerging for cutaneous reflex control during arm cycling is quite similar to that observed in leg muscles during leg cycling or walking (Zehr and Kido 2001); cutaneous reflexes in most arm muscles are extensively phase- and task-modulated (i.e., static vs. movement). The observation that cutaneous reflexes were task-dependent (some even showing reflex reversal) suggests that a central pattern or rhythm generator may be involved in controlling reflex pathways during arm cycling movement in humans (Zehr and Kido 2001).

Currently there are few papers that address the modulation of reflexes arising from muscle afferents (e.g., H-reflexes) during human arm cycling movement. It has been shown that long-latency stretch reflexes of triceps brachii and brachialis are modulated continuously throughout a rhythmically reciprocating elbow flexion-extension movement (MacKay et al. 1983). However, active contralateral arm movement failed to significantly modulate the H-reflex of the ipsilateral flexor carpi radialis (FCR) H-reflex (Delwaide et al. 1988). Rhythmic active and passive movement of the contralateral wrist has been shown to induce significant suppression of FCR H-reflex amplitude (Carson et al. 1999). More recently, passive flexion-extension movement of the ipsilateral wrist or elbow was also shown to significantly inhibit H-reflex amplitude in FCR muscle (Brooke et al. 2000). However, the general pattern of H-reflex modulation during rhythmic whole arm movement remains incomplete. The purpose of the present research was to identify the pattern of H-reflex modulation in forearm muscles during arm cycling and to compare these observations to what is known to exist for the human leg. We hypothesized that H-reflexes would show both phase dependence (i.e., modulated by position in the movement cycle) and task modulation (i.e., smaller during movement as compared with static contraction) as has been documented for the leg. Further we aimed to determine the locus of any modulation by examining independent arm movement and active and passive movement of each arm. Portions of this data have been presented previously (Zehr et al. 2001a).

METHODS

Subjects

Sixteen subjects, who ranged in age from 23 to 38 yr and were free from documented neurological disease, participated in the experiments with informed written consent. Nine subjects participated in each of two main sets of experiments. The project was conducted under the sanction of the Human Research Ethics Board (Panel B) at the University of Alberta and performed according to the Declaration of Helsinki.

Protocol

The general experimental methodology and protocol are similar to that described in previous experiments involving arm cycling and cutaneous reflex modulation (Zehr and Chua 2000; Zehr and Kido 2001). Subjects performed rhythmic arm cycling on a custom-made (Z. Kenwell, University of Alberta) hydraulic arm ergometer. The handles of this ergometer were mounted to two hydraulic pumps that provided an adjustable but constant resistance. The resistance was set to produce muscle activation in the upper limb without causing undue fatigue (~170–340 kPa). Both arms could be constrained to move together (e.g., handles fixed together) or could be moved independently. For all trials, the subjects held the handgrips firmly but comfortably with the forearms pronated.

Subjects performed two main tasks: rhythmic arm cycling and static contraction with the arms stationary. The arm cycling task was subdivided into bilateral and unilateral and active and passive movement. The position of the ergometer cranks was determined from a linear continuous turn potentiometer that was reset with each movement cycle. In all movement conditions, subjects were instructed to cycle at a comfortable rate (~60 rpm). The movement cycle was defined relative to the clock face (see Fig. 1). The position when the ipsilateral handle was straight up corresponded to 12 o'clock with positional definitions continuing clockwise. Reflexes during arm cycling and stationary contraction were evoked at four equidistant positions in the movement cycle (12, 3, 6, and 9 o'clock) chosen to include positions of maximal flexion (3 o'clock) and extension (9 o'clock) of the stimulated limb and two intermediate positions.

The experiments were conducted in two sets with nine subjects participating in each set (note that 2 subjects participated in both parts). In the first set of experiments, the phase and task dependence of H-reflexes was evaluated during bilateral arm cycling and static contraction at similar ipsilateral FCR (iFCR) EMG levels for each of the four positions described above. The locus of movement-induced reflex modulation was evaluated in the second set of experiments. H-reflexes were evoked only at one position (6 o'clock) for all conditions in this set of experiments. This position was chosen because it was one of the two positions where there was a significant difference between control and movement trials in the first set of

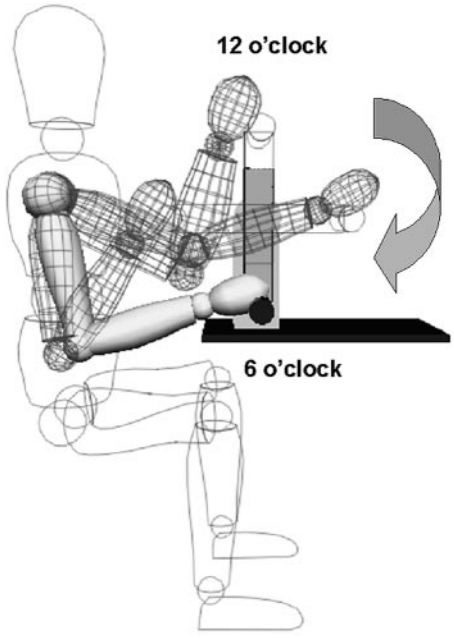

FIG. 1. Schematic indicating the approximate positions of the ipsilateral arm when the handle was at 12, 3, 6, and 9 o'clock positions. Arrow indicates clockwise direction of rotation.

experiments. In these subjects, the effect of ipsilateral and contralateral arm movement was examined. Both movements were done in active (IPSI and CONTRA) and passive ($IPSI_{passive}$ and $CONTRA_{passive}$) conditions. For passive movement, the arm of the subject was moved by the experimenter at a similar frequency and with a similar orientation as recorded during active movement. In all conditions, subjects maintained a similar tonic level of activity in the forearm flexor muscles using feedback of the rectified signal from iFCR. For active movement, subjects were instructed to perform rhythmic voluntary arm cycling with either the ipsilateral or contralateral arm. Also in these nine subjects, the effect of varying the forearm flexor muscle EMG level was examined by holding two different levels (low and high) of voluntary contraction while reflexes were evoked at 6 o'clock for stationary and bilateral arm cycling tasks. The order in which the tasks were performed was randomized for each subject.

Nerve stimulation

Nerve stimulation (Grass S88 stimulator connected in series with an SIU5 isolator and a CCU1 constant current unit, Grass Instruments, AstroMed) was delivered approximately once every three cycles during movement and pseudorandomly between 1 and 3 s during static contraction. This stimulus regime enabled sufficient data to be collected during the ~2-h data-collection period to permit the construction of recruitment curves for all conditions. The median nerve was stimulated with single 1.0-ms pulses applied through bipolar surface electrodes placed just proximal to the medial epicondyle of the humerus on the right arm. Appropriate stimulation location was checked by determining that twitch responses were evoked in appropriate wrist flexor muscles (e.g., FCR) and that a pronounced and radiating tingling into the lateral portion of the palmar surface of the hand could be detected on increasing stimulus intensity. Direct muscle activation (M-wave) and H-reflexes were evoked from FCR in all conditions, and stimulation current was also measured (mA-2000 Noncontact Milliammeter, Bell Technologies, Orlando Fl). M-H recruitment curves were obtained in all conditions by applying stimulation current over a range of intensities from subliminal for any response up to that which evoked a maximal M-wave (M_{max})(Zehr and Stein 1999a; Zehr et al. 2001b). In all, 75 stimuli were delivered to generate M-H recruitment curves for each subject for each experimental condition. To minimize effects of changes in forearm flexor muscle length, subjects wore a wrist brace on the hand of the stimulated arm. This brace significantly reduced wrist movement amplitude and helped maintain stimulus stability (see Zehr and Kido 2001).

Electromyography

Muscles studied included flexor carpi ulnaris (FCU), extensor carpi ulnaris (ECU), FCR, pronator teres (PT), anterior deltoid (AD), posterior deltoid (PD), and biceps brachii (BB). Not all muscles were studied in every subject except for AD and FCR (which were always recorded bilaterally). EMG signals were preamplified and band-pass filtered at 30–300 Hz (P511 Grass Instruments, AstroMed). With the exception of the iFCR, EMG recordings were full-waved rectified.

In addition to the sampling at the four positions of the movement cycle during all H-reflex conditions, EMG was also collected across the entire movement cycle. These data were used to create ensemble averages (based on a minimum of 10 cycles) of EMG patterns for the whole movement cycle for all subjects and tasks.

Kinematics

In all subjects, kinematic recordings of elbow joint angles were obtained from both arms using lightweight goniometers (Biometrics). From the elbow joint trajectories, range of motion and average velocity across the movement cycle for all tasks were calculated.

Data acquisition and analysis

Data were acquired at a sampling rate of 5,000 Hz with a 12 bit A/D converter connected to a computer running custom-written (Dr. Romeo Chua, University of British Columbia) LabView (National Instruments) virtual instruments. For all H-reflex conditions, 75 sweeps of data were collected. Sweep length was set at 70 ms with a 30-ms prestimulus window.

EMG analysis

EMG ACTIVITY DURING MOVEMENT. The level of muscle activation during the different motor tasks and at the different positions was determined with an analysis of background EMG amplitudes from H-reflex trials. In these trials, the prestimulus (30 ms) EMG was rectified and averaged to provide a mean level of muscle activation during reflex sampling. Additionally, to determine the EMG patterns when performing the different types of arm movements (e.g., IPSI vs. bilateral), EMG patterns were obtained from 12 hourly positions throughout the entire movement cycle (e.g., 12, 1, 2, 3, 4 o'clock, etc).

H-REFLEXES. H-reflex analysis was conducted off-line (using custom-written software, Matlab, Nantick) on the single unrectified sweeps of FCR EMG. The data were superimposed, and windows were set to define the epochs for the M-waves and H-reflexes. The peak-to-peak amplitudes of each M-wave and H-reflex were then calculated along with the average of the rectified prestimulus EMG for each muscle. The integral of the stimulating current was calculated to yield a stimulus charge value for each pair of corresponding M-waves and H-reflexes. The maximal M-wave amplitude (averaged over the 3 largest values obtained) in each condition was determined and used to calibrate the entire M-H curve for each condition for a given subject. These normalized M-H pairs were then plotted, and analysis was conducted at three places (ascending limb, H_{max}, and descending limb) on the recruitment curve. Approximately 10–20 sweeps from the ascending and descending limb of the recruitment curve were typically used to construct averages while H_{max} was calculated from an average of the three largest H-reflexes recorded. For reflexes on the ascending limb, the same relative M-wave amplitude was used across all conditions within a subject (e.g., H-reflex amplitude at 5–10% M_{max} was compared in all conditions for a given subject). Furthermore, H-reflexes at the mid-way point on the descending limb of the M-H curve (e.g., 15–25% M_{max}) were also examined. These procedures allowed us to assess the extent to which reflex size affects H-reflex conditioning in the arms as has been addressed recently during leg cycling (Zehr et al. 2001b).

Statistics

Statistical analysis was conducted on data across all subjects. ANOVA was used to determine main effects and to ascertain significant differences between tasks (e.g., movement vs. stationary, IPSI vs. bilateral, etc.) as well as phase dependency within a task (e.g., 12, 3, 6, and 9 o'clock). Planned comparisons were used to evaluate differences between conditions. Tukey's HSD test was used to post hoc significant main effects. Descriptive statistics included means ± SE. Statistical significance was set at $P \leq 0.05$.

RESULTS

Background EMG patterns during arm cycling

Plotted in Fig. 2 are the EMG patterns from six muscles across the 12 hourly positions of the entire movement cycle for each task. For iFCR muscle, EMG levels for IPSI and $IPSI_{passive}$ were not significantly different from bilateral cycling. For the other muscles, generally when the arms were moved during one armed (either IPSI or CONTRA) cycling,

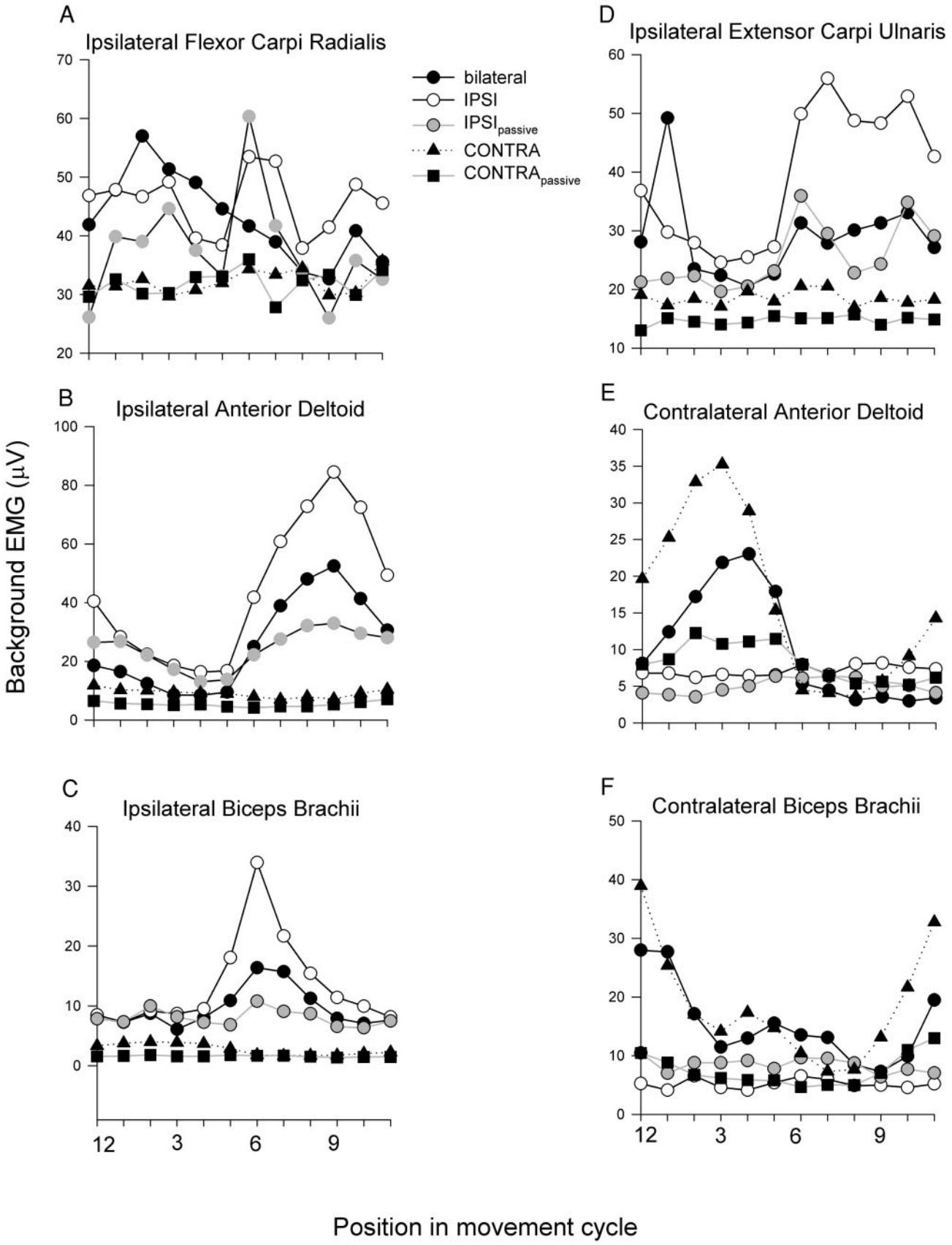

FIG. 2. Background electromyographic (EMG) patterns measured across the 12 positions of the movement cycle for all 5 arm cycling conditions. Shown are mean values from all 9 subjects during constrained bilateral arm cycling (bilateral, ●), active movement of the ipsilateral arm only (IPSI; ○), ipsilateral arm passive ($IPSI_{passive}$, ◎) and contralateral arm active (CONTRA; ▲), and passive ($CONTRA_{passive}$; ■). Error bars have been omitted for clarity.

EMG levels in the active moving limb were significantly higher ($P < 0.01$) than those levels seen in that limb during bilateral cycling. Furthermore, EMG amplitudes across the whole movement cycle for iBB, cBB, iFCR, iECU, iAD, and cAD (i-, ipsilateral; c-, contralateral) were significantly lower ($P < 0.01$) during passive movement than during active single arm movements.

EMG amplitudes during H-reflex trials

In the first set of experiments, data were sampled at the four positions during bilateral cycling and while subjects remained stationary. Planned comparisons revealed that iFCR EMG was significantly ($P < 0.05$) higher during cycling than while static at 3 o'clock (see Fig. 4*C*). Otherwise, iFCR EMG amplitudes were not significantly affected by task (i.e., cycling vs. static contraction) or position in the movement cycle. For the other muscles, there were typically no statistically significant differences in muscle activation levels at 12, 3, 6, and 9 o'clock positions either while moving or during static contraction (i.e., no main effects for task or position). However, iAD showed a significant main effect for task and iFCU for position. Planned comparisons revealed that EMG levels were higher during cycling in iAD (6 and 9 o'clock positions) and cFCR (12 and 9 o'clock). Thus the general feature was that EMG levels were similar when comparing bilateral cycling and static contraction across the four positions studied in the first set of experiments.

In the second set of experiments, reflexes were sampled at 6 o'clock during the six different tasks. iFCR EMG amplitudes in IPSI were significantly higher ($P < 0.05$) than static and significantly lower in $CONTRA_{passive}$ than IPSI. There were no other significant differences in iFCR EMG across tasks. In other muscles, there were significant effects of the motor task on EMG amplitudes. These are summarized in Table 1. The analysis presented in Table 1 indicates whether EMG activity at 6 o'clock for a given condition changed significantly across tasks in the recorded muscles. One can begin with any condition on the left-hand side and read across the columns to determine if there was a significant change in EMG activity. For example, starting at the top left with static, it can be seen by moving to the right that EMG amplitudes in iAD during static were significantly lower than those seen during bilateral, IPSI, and $IPSI_{passive}$. The general feature that emerges from the Table is that iAD and iBB activity were often significantly elevated during ipsilateral arm movement.

Elbow joint kinematics

Joint excursion at the elbow during cycling movements ranged from 69.5 to 72.2° across conditions (NS). Further, there were no significant differences in average elbow velocity between the different movement conditions (range: 169.9–186.7°/s).

H-reflex amplitude during static contraction versus bilateral cycling

H-reflexes taken from the ascending limb of the M-H curve, were significantly (main effect for task; $P < 0.01$) smaller during arm cycling as compared with static contraction (see Figs. 3*A* and 4*A*). Additionally, there was a significant modulation of H-reflex amplitude by position (main effect for position; $P < 0.005$; Figs. 3*B* and 4*A*). In Fig. 3*B*, data from a single subject for all four cycle positions are plotted together. Open symbols are those from static contraction and filled ones are those from cycling. The different symbols represent data

TABLE 1 *Significant changes in EMG activity during the different tasks*

	Static	Bilateral	IPSI	IPSI passive	CONTRA	CONTRA passive
Static		iAD*** iBB*** ↓	iAD*** iBB*** iECU*** iFCR* ↓	iAD*** ↓		cAD* ↓
Bilateral			iAD*** iBB** ↓		iAD*** iBB*** ↑	iAD*** iBB*** ↓
IPSI				iAD*** iBB*** ↑	iAD*** iBB*** iECU* ↑	iAD*** iBB*** iECU*** iFCR* ↑
IPSI passive					iAD** ↑	iAD** ↑
CONTRA						
CONTRA passive						

The table should be read from left to right, and arrows indicate the direction of change for the leftmost column. Statistical significance is as indicated. Empty cells indicate no significant differences in electromyography (EMG). IPSI and CONTRA, ipsi- and contralateral; iAD, ipsilateral anterior deltoid; iBB, ipsilateral biceps brachii; iECU, ipsilateral extensor corpi ulnaris; iFCR, ipsilateral flexor corpi ulnaris. *$P < 0.05$; **$P < 0.01$, ***$P < 0.005$.

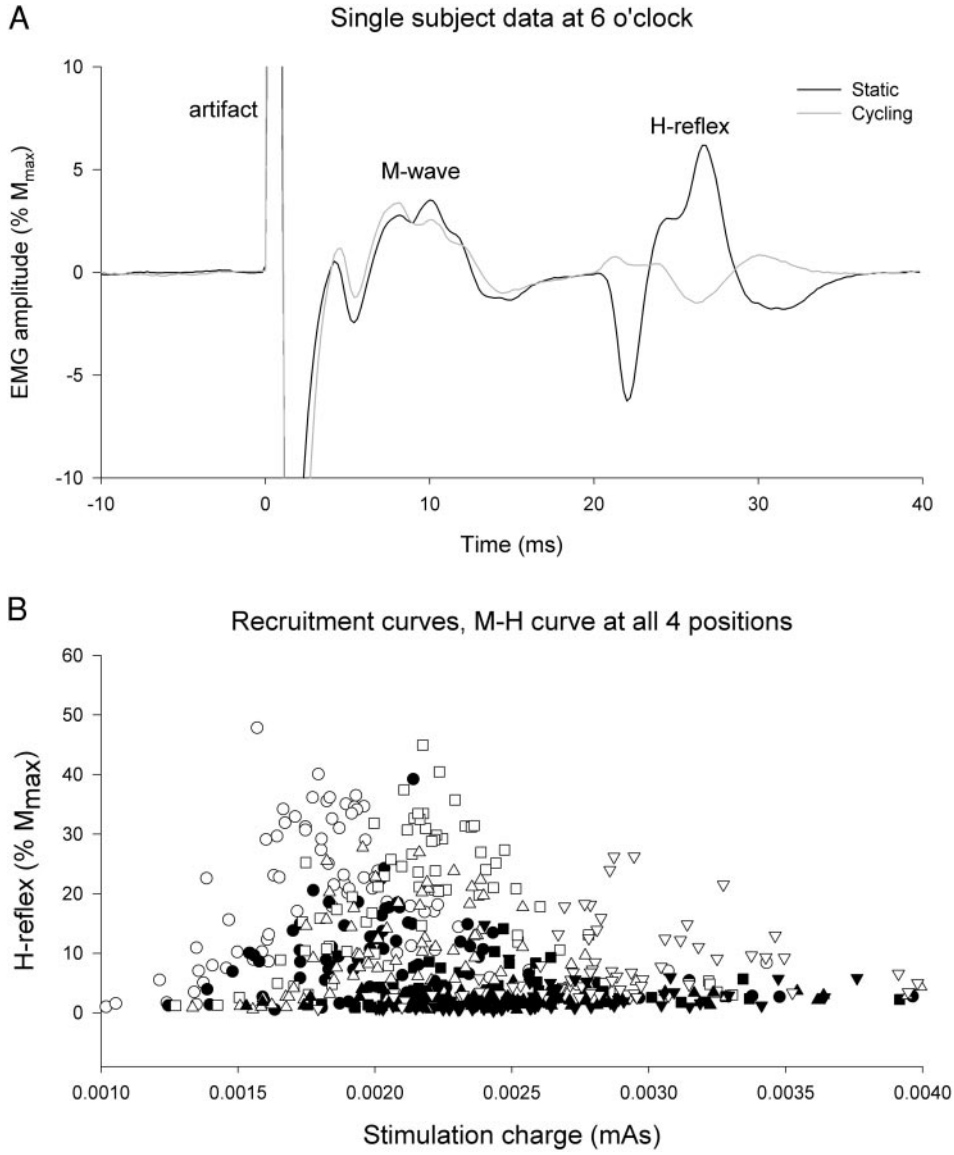

FIG. 3. Task-dependent attenuation of forearm Hoffmann (H-) reflex amplitude in a single subject. *A*: average data taken from the ascending limb of the M-H recruitment curve for during cycling and static contraction sampled at the 6 o'clock position. *B*: H-reflex recruitment curves across all 4 movement positions (○, □, △, and ▽ indicate 12, 3, 6, and 9 o'clock, respectively) for both static (○, □, △, ▽) and movement (●, ■, ▲, ▼) conditions. The different positions have been combined to give an indication of the generalized effect of H-reflex suppression during movement.

taken from the four positions (see legend). The main observation from these data are that, irrespective of position in the movement cycle, H-reflexes were suppressed during bilateral cycling movement compared with static contraction. For the group, planned comparisons revealed that H-reflexes at 6 and 9 o'clock were significantly smaller during cycling as compared with static contraction (see Fig. 4*A*). There were no significant differences in M-wave (Fig. 4*B*; mean M-wave $=7.74 \pm 1.8\%$ M_{max}) or FCR EMG (Fig. 4*C*) amplitudes across any of the movement positions or in static or cycling tasks.

Reflex amplitudes taken at H_{max} and from the descending limb showed similar features as those from the ascending limb. This movement-related reduction of reflex magnitude, across the full range of stimulation intensities, can be seen for an individual subject by comparing symbols in Fig. 3*B* (○, □, △, and ▽ vs. ●, ■, ▲, and ▼). For the group, H_{max} amplitudes were significantly smaller during cycling (main effect $P < 0.05$). There was no significant effect of position in the movement cycle, but there was a significant interaction ($P < 0.05$) that revealed that H_{max} values at 9 o'clock were significantly smaller during cycling as compared with static contraction ($P < 0.01$). H-reflexes from the descending limb of the M-H curve were smaller during cycling compared with static contraction and showed both task ($P < 0.01$) and phase dependence (6 and 9 o'clock were different from static; $P < 0.05$) modulation. Just as for reflexes sampled on the ascending limb, both M-wave amplitudes ($26.79 \pm 5.46\%$ M_{max} on the descending limb) and FCR EMG levels were of constant size across all conditions.

H-reflex amplitude in static contraction versus different arm cycling tasks

H-reflexes were task-dependently modulated such that reflexes recorded during bilateral cycling were significantly smaller than those obtained during static contraction (main effect for task, $P < 0.01$). To explore the task dependence further, we compared H-reflex amplitudes evoked during static contraction at 6 o'clock to those obtained during bilateral cycling and with movement of either the ipsilateral or contralateral arms. As shown in Fig. 5, reflexes on the ascending limb were significantly (main effect for task, $P < 0.001$)

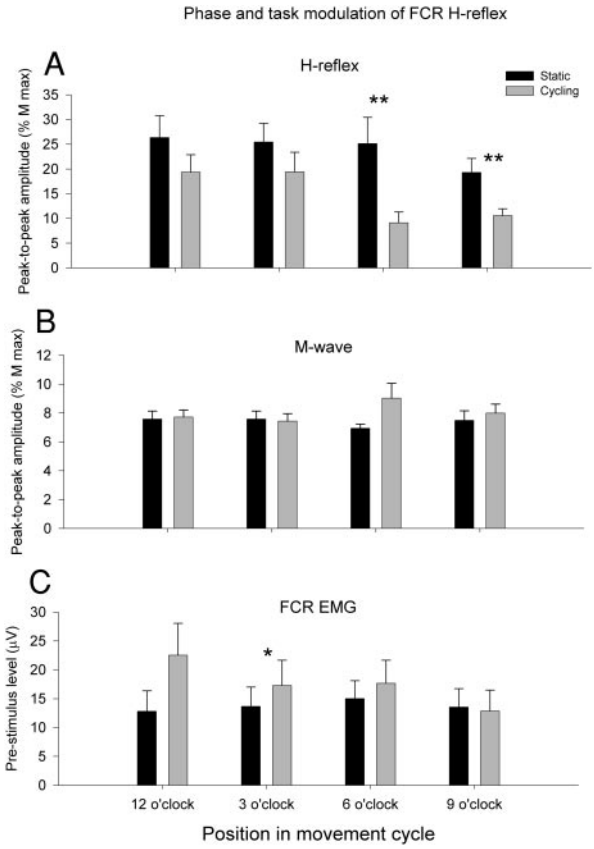

FIG. 4. H-reflex (*A*), M-wave (*B*), and FCR EMG (*C*) data are shown averaged across all subjects. There was a significant effect of task for H-reflex amplitude, but no difference in M-wave amplitude and FCR EMG level (except at 3 o'clock) between conditions. Values are means ± SE for 9 subjects. * and **, significant differences as tested with planned comparisons at $P < 0.05$ and $P < 0.01$, respectively.

reduced in amplitude compared with static contraction for bilateral (50.8% reduction in amplitude, $P < 0.005$), IPSI (65.3%, $P < 0.001$), and $IPSI_{passive}$ (52.6%, $P < 0.001$) arm cycling. The amount of inhibition during these three tasks was not significantly different. Both active and passive contralateral

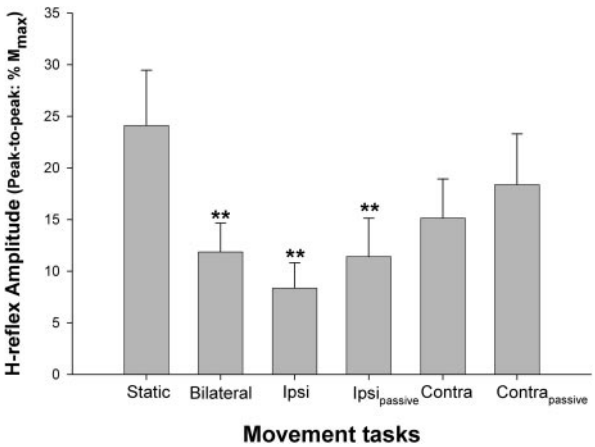

FIG. 5. Task-dependent modulation of the forearm flexor H-reflex. H-reflexes were significantly smaller during bilateral, and ipsilateral active (IPSI) and passive ($IPSI_{passive}$) arm cycling compared with static contraction. In these 3 tasks, there was no difference in M-wave amplitude or FCR EMG levels (not shown). Values are means ± SE for 9 subjects. **, significant differences from static H-reflex amplitudes at $P < 0.01$.

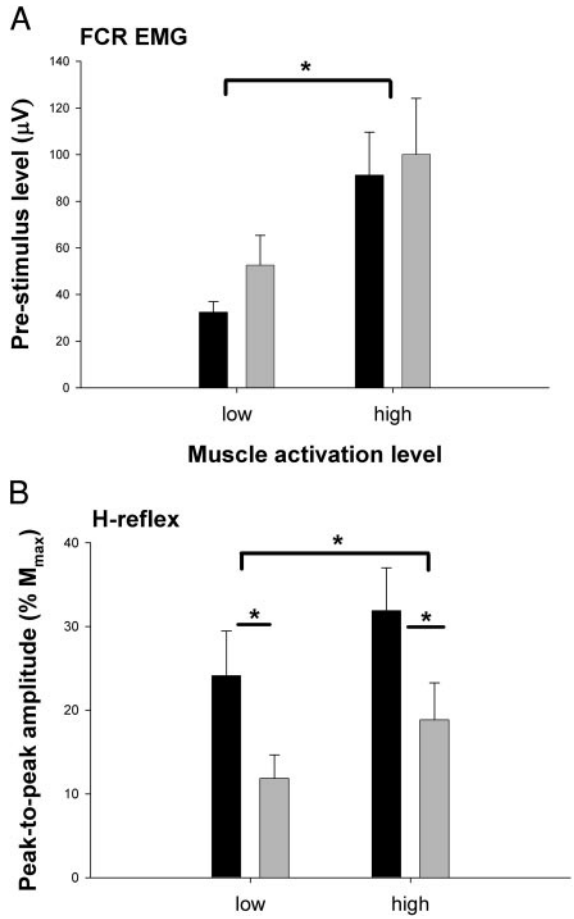

FIG. 6. The effect of low and high levels of EMG activity (*A*) on peak amplitude of the forearm H-reflex (*B*) during static (black bars) and movement (gray bars) trials. M-wave amplitudes were matched across conditions. Despite similar increases in EMG in both static and movement trials, H-reflexes were significantly smaller during cycling. However, H-reflexes with a high contraction level were significantly larger than those with a low level. *, significant differences between static and movement at $P < 0.05$. Values are means ± SE for 9 subjects.

cycling failed to suppress the H-reflex amplitude significantly. Interestingly, the inhibition of H-reflex amplitude in the IPSI condition occurred despite a significantly increased ($P < 0.05$) iFCR EMG amplitude compared with static (see Table 1). M-wave amplitudes were not significantly different. Similar patterns were observed when H_{max} and reflexes from the descending limb were examined (not shown).

Effect of iFCR EMG level on H-reflex amplitude

For these experiments, subjects were requested to hold a low and high EMG level in iFCR muscle during static contractions and rhythmic movement. EMG amplitudes were significantly greater ($P < 0.03$) during the high contraction condition (42.1% MVC) as compared with the low level contraction (20.6% MVC; see Fig. 6*A*), but there was no significant effect of task on EMG amplitude. Thus EMG amplitude during cycling was closely matched with EMG during static contraction. Forearm H-reflex amplitude was significantly larger ($P < 0.002$) in the high contraction condition than the low contraction condition (see Fig. 6*B*). Further, H-reflex amplitude was significantly smaller ($P < 0.05$) during cycling as compared

with static contraction (there was no significant interaction). Planned comparisons revealed that H-reflexes were smaller during movement at both the low ($P < 0.02$) and high ($P < 0.01$) muscle activation levels. There were no significant differences in M-wave size between any of the four conditions. This effect of EMG level on H-reflex amplitude for data taken from the ascending limb was generally paralleled at both H_{max} and the descending limb of the M-H curve.

DISCUSSION

The main observation from the present experiments is that the amplitude of H-reflexes in forearm flexor muscles is significantly reduced during rhythmic arm movements compared with static contraction. Interestingly, bilateral cycling and active and passive movement of the stimulated limb reduced H-reflex amplitude to the same extent, whereas contralateral movement failed to significantly affect H-reflex amplitude. Thus H-reflexes are task-dependent during rhythmic movement of the upper limb. These observations are consistent with our previous results on task-dependent modulation of cutaneous reflexes during arm cycling (Zehr and Kido 2001). The current paper represents the first rigorous quantification and documentation of H-reflexes during rhythmic whole arm cycling movement and also extends the description of reflex modulation to active and passive movements of the single upper limb.

Methodological issues

In studies examining changes in H-reflex amplitudes there are numerous methodological issues that require careful attention (for reviews see Brooke et al. 1997 and Zehr 2002). Of particular concern are the effects of differential conditioning on reflexes of different size, constancy of nerve stimulation, constancy of motoneuronal pool depolarization, and movement velocity. These will be addressed in turn. First it has been shown that, due to the differences in the populations of motor units involved, small and large H-reflexes are differentially sensitive to excitatory and inhibitory conditioning (Crone et al. 1990). Thus it is important to examine reflexes of different amplitudes to evaluate the effect of different sources of conditioning. Therefore we presently selected H-reflexes from three points in the M-H curve as in an earlier study in the lower limb (Zehr et al. 2001b). Interestingly, just as with the soleus H-reflex (Zehr et al. 2001b), the general features of modulation of the forearm flexor H-reflex were essentially the same at all three points. Thus when movement is the conditioning source the size of the so-called "test" reflex does not seem to play a very large role in contrast to conditioning evoked in different somatosensory pathways (Crone et al. 1990). This discrepancy may arise because movement evokes global changes affecting inputs to the whole pool of motor neurons, whereas restricted somatosensory conditioning inputs may affect certain subsets of neuronal pools differentially. Second, the size of the M-wave amplitude has typically been used as an index of stimulus constancy (Brooke et al. 1997; Mayer and Mawdsley 1965). Typically, H-reflex and M-wave amplitudes are normalized to M_{max} (see Zehr 2002 for discussion). However, there is evidence that M_{max} values can change over time within an experiment (Crone et al. 1999) and at different limb positions (Ferris et al. 2001; Gerilovsky et al. 1989). Thus it is important to normalize to M_{max} values within a condition across an experiment. In this study, we did this in every experimental condition and compared H-reflexes only when the normalized M-wave amplitudes were matched. Thus stimulus constancy and subtle changes in maximal M-wave amplitudes were controlled. Third, fluctuations in the level of target motoneuronal pool depolarization (e.g., the forearm flexors in this experiment) can act as a significant confounding influence. However, in the current study, we controlled the amplitude of the forearm flexor muscle activation to reduce this as a possible influence. Fourth, it has been shown that velocity of movement has a significant effect on soleus H-reflex amplitude during leg cycling (Cheng et al. 1995). In the present study, subjects cycled at a similar velocity during all movement tasks, and there were no significant differences in range of motion or velocity of movement. Thus differences in movement velocity (and indirectly muscle stretch) cannot account for our observations. Finally, the interstimulus interval presently used (1–3 s) was slightly higher than that recommended to avoid lasting effects from prior stimulus pulses (5–8 s) (see Brooke et al. 1997). However, similar interstimulus intervals were used for all conditions in the present study, thus any lasting effects will have been similar across conditions and could not account for the task and phase dependency shown presently. In summary, the methodological procedures adhered to in this paper allow us to have confidence that the observed changes in forearm flexor H-reflex amplitudes were not the result of methodological error.

Potential heteronymous influences on H-reflex amplitude

For H-reflexes during leg cycling, active and passive movements have been used to evaluate the relative contribution to the observed reflex modulation of peripheral feedback arising from movement and central motor commands (for review, see Brooke et al. 1997). Here we used a similar approach during arm cycling. To have the cleanest separation of the possible contributions from these sources, it would be preferable to have quiescence in all motor pools except for the target muscle iFCR. However, as can be seen in Fig. 2 and Table 1, the other muscles were not electromyographically silent during passive movement. This likely arose from the difficulty subjects experienced in trying to maintain a constant EMG level in iFCR while allowing passive movement of the limb. While there was EMG activity in other muscles during passive movement, the passive movements were involuntary and this EMG activity did not arise from deliberate voluntary motor commands.

Other concerns associated with changes in EMG amplitude across tasks are the effects of reciprocal inhibition and other heteronymous effects such as recurrent inhibition. For the first set of experiments, there were negligible differences in EMG between static and cycling at the four positions. However, for the second set of experiments in which the amplitude of FCR H-reflex were compared across the six tasks, there were significant changes in EMG activity in some muscles (see Table 1). A major consideration is the effect of reciprocal inhibition of FCR H-reflex estimated from antagonist (e.g., iECU) muscle activity (Baldissera et al. 1983; Cody and Plant 1989; Day et al. 1984). Indeed, compared with static levels, iECU EMG activity was significantly elevated during the task that showed the largest inhibition (IPSI). However, iECU was not significantly

elevated during bilateral or $IPSI_{passive}$, the two other tasks that showed significant inhibition of FCR H-reflex. We thus do not feel that reciprocal inhibition, as estimated from antagonist EMG activity, was the major source of H-reflex inhibition across tasks here. Another heteronymous source could be recurrent inhibition from other arm muscles such as iBB and iAD (the EMG from both of which were significantly affected by task; Table 1). However, it was shown that muscles acting at the wrist do not receive heteronymous recurrent inhibition from proximal muscles acting at the shoulder or elbow (such as AD and BB) (Katz et al. 1993). There is, though, a heteronymous effect (likely mediated by group IA afferents) from BB onto FCR that could inhibit H-reflex amplitude (Cavallari et al. 1992). It is possible that this could have contributed to the presently observed inhibition of the FCR H-reflex. However, there was no consistent pattern of changes in muscle activation in all conditions (see Table 1 and a lack of significant change in iBB activity and yet a significant H-reflex inhibition during $IPSI_{passive}$). The only consistent feature was that of movement. We suggest that, while these other factors could certainly contribute to the observed modulation, they are not the dominant source.

H-reflex modulation during arm movement

Our results are consistent with previous data on modulation of reflexes arising from muscle afferents during rhythmic arm movement. It was previously shown that stretch reflexes in BB and brachialis muscles were modulated during the performance of cyclical reciprocating flexion-extension movements at the elbow (MacKay et al. 1983). While these movements were not performed continuously (they were flexion-stop-extension-stop, etc.), the general observation of movement-induced modulation of muscle afferent reflexes in the upper limb is the same as our observations for rhythmic arm movements. In a study directly comparable to the present study, Delwaide et al. (1988) found that rhythmic, cyclical movement of the contralateral arm performed either actively or passively did not affect the FCR H_{max}. We also found that contralateral movement (whether active or passive) failed to suppress the H-reflex (regardless of which place on the M-H curve was analyzed) but ipsilateral movement did. Movement of individual joints in the ipsilateral limb have also been shown to alter H-reflex amplitudes. Forearm H-reflexes are highly modulated by rhythmic wrist movement (Carson et al. 1999), but this may have been due to differences in EMG activity of the forearm musculature. Also, irregular flexion-extension movements at the wrist or elbow significantly reduced the amplitude of FCR H-reflexes and somatosensory evoked potentials (Brooke et al. 2000).

Comparison to the leg

Previously we documented that cutaneous reflexes from the three main nerves innervating the hand were phase- and task-modulated during arm cycling (Zehr and Chua 2000; Zehr and Kido 2001). Cutaneous reflexes are not significantly modulated by limb position during static contractions (Zehr and Kido 2001), and our results here extend this observation to forearm H-reflexes. Thus cutaneous and H-reflexes are phase modulated during arm cycling movement as has previously been documented in the lower limb during leg cycling (Brooke et al. 1999; see for review Brooke et al. 1997). Interestingly, the largest suppression of H-reflex amplitude in the leg is during the so-called "recovery phase" in which the knee is flexing, and there is strong stretch of the knee extensor muscles (Cheng et al. 1995). Similar orientation of the upper limb during our arm cycling paradigm would be 6 and 9 o'clock. At these positions, the elbow extensors are stretched to the largest extent, and these are the positions at which the largest suppression of forearm H-reflex amplitude was measured. We presently found that forearm H-reflexes were not inhibited during the extension phase of arm cycling, compared with static contractions, which is also consistent with previous results showing a lack of inhibition of soleus H reflexes during the extension phase of leg cycling (Zehr et al. 2001b). Thus when the stimulated limb moves, there is a similar phase-dependent modulation of H reflexes in the upper and lower limb.

The general feature of task-dependent modulation of forearm H-reflexes is consistent with observations on H-reflexes (soleus and tibialis anterior) during leg cycling. We found that any movement involving the ipsilateral limb had a significant inhibitory effect; however, there was no effect of contralateral arm movement. This is somewhat different from what is seen in the leg wherein there is a strong effect of contralateral movement, even during passive leg movement (Cheng et al. 1998). Thus regulation of transmission in muscle afferent pathways evaluated by H-reflex stimulation is only partially similar to that seen in the leg. In the arm it seems that the movement context of the stimulated limb has priority in modulating the amplitude of the H-reflex in forearm flexor muscles.

Mechanisms of reflex modulation during arm cycling movement

In the lower limb, the patterns of cutaneous and H-reflex modulation are suggestive of activity in central-pattern–generating (CPG) networks associated with leg movement (Brooke et al. 1999; Zehr et al. 2001b). Extensive phase and task dependency of cutaneous reflexes during arm cycling suggests that there is also a CPG controlling rhythmic arm movement (Zehr and Kido 2001). The presently observed patterns of modulation of the forearm H-reflex suggest that CPGs associated with arm movement control separately each limb as might be predicted based on recent distributed segment models of CPG networks (e.g., unit burst generators) (Duysens 1998; Duysens and Van de Crommert 1998; Kiehn et al. 1997; Pearson 2000; Pearson and Ramirez 1997; Stein and Smith 1997). However, there are some differences in the patterns between the arms and legs (e.g., lack of contralateral effect on H-reflex amplitude in the arms). It is known that CPGs controlling leg movements are closely coupled in quadrupedal mammals (Hultborn et al. 1998; MacKay-Lyons 2002). Possibly this tight coupling exists as well in bipedal humans who typically use the legs in bilateral movements such as in reciprocating gait. In the upper limb, this coupling may not be as tight due to the more frequent independent use of the arms. Additionally, because passive movement of the ipsilateral limb reduced H-reflex amplitude, it is likely that peripheral feedback related to movement of the limb is involved. However, it is not possible to rule out an interaction between peripheral feedback and centrally generated outflow in controlling reflex amplitude. Here we observed that H-reflexes scaled with background

EMG during both static contraction and during arm cycling, the level of movement-induced H-reflex inhibition during arm cycling was roughly constant at ~40% for both contraction levels (see Fig. 6). This suggests a mechanism that is evenly distributed to inputs to the whole neuronal pool and has a global effect. A likely candidate mechanism is presynaptic inhibition as has been suggested for the control of muscle afferent reflexes in the leg (Brooke et al. 1997; Stein 1995).

In summary, the inhibition of H-reflex amplitude during bilateral and ipsilateral arm cycling compared with static contraction suggests that feedback from the moving arms and central mechanisms (possibly originating from a CPG resident in the cervical spinal cord) both interact to modify peripheral feedback during arm movements.

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