Neural control of rhythmic, cyclical human arm movement: task dependency, nerve specificity and phase modulation of cutaneous reflexes

E. Paul Zehr *† and Aiko Kido†

*Neurophysiology Laboratory, Faculty of Physical Education & Recreation
and † Centre for Neuroscience, University of Alberta, Edmonton, Alberta, Canada*

1. The organization and pattern of cutaneous reflex modulation during rhythmic cyclical movements of the human upper limbs has received much less attention than that afforded the lower limb. Our working hypothesis is that control mechanisms underlying the modulation of cutaneous reflex amplitude during rhythmic arm movement are similar to those that control reflex modulation in the leg. Thus, we hypothesized that cutaneous reflexes would show task dependency and nerve specificity in the upper limb during rhythmic cyclical arm movement as has been demonstrated in the human lower limb.

2. EMG was recorded from 10 muscles crossing the human shoulder, elbow and wrist joints while bilateral whole arm rhythmic cyclical movements were performed on a custom-made, hydraulic apparatus.

3. Cutaneous reflexes were evoked with trains (5×1.0 ms pulses at 300 Hz) of electrical stimulation delivered at non-noxious intensities ($\sim 2 \times$ threshold for radiating parasthesia) to the superficial radial, median and ulnar nerves innervating the hand.

4. Cutaneous reflexes were typically modulated with the movement cycle (i.e. phase dependency was observed). There was evidence for nerve specificity of cutaneous reflexes during rhythmic movement of the upper limbs. Task-dependent modulation was also seen as cutaneous reflexes were of larger amplitude or inhibitory (reflex reversal) during arm cycling as compared to static contraction.

5. While there are some differences in the patterns of cutaneous reflex modulation seen between the arms and legs, it is concluded that cutaneous reflexes are modulated similarly in the upper and lower limbs implicating similar motor control mechanisms.

While the organization and patterns of modulation of cutaneous reflexes have been shown to be quite similar when comparing the fore- and hindlimbs in the cat (Drew & Rossignol, 1987), very little study of cutaneous reflexes during human upper limb rhythmic movement has been made. An important feature of cutaneous reflex control seen in the human lower limb during locomotion is task dependency. Task dependency refers to the changes in amplitude and sign of a reflex that can be observed when sampling in different motor tasks. For example in leg muscles, task dependency of cutaneous reflexes has been shown at similar EMG levels in standing *vs.* walking (Komiyama *et al.* 2000), standing *vs.* running (Duysens *et al.* 1993), cycling *vs.* static contraction (Zehr *et al.* 2001) and stable *vs.* unstable standing (Burke *et al.* 1991). The main observation from these experiments is that cutaneous reflexes in leg muscles are very sensitive to the specific motor task that is performed and that rhythmic movements, as compared to static contractions, have

distinctly different reflex patterns. The extent to which cutaneous reflexes in the upper limb also display features of task dependency between static and rhythmic muscle activation is unclear.

Another feature of cutaneous reflexes in the lower limb is nerve specificity (also 'location specificity'; Van Wezel *et al.* 1997). Nerve specificity refers to the observation that reflexes of different sign and in different muscles can be evoked after stimulation of cutaneous nerves innervating different areas of the human foot (Zehr *et al.* 1997, 1998; Van Wezel *et al.* 1997). That is, nerve specificity represents the functional outcome of different reflex connections from different cutaneous nerves onto the same muscles. These different reflexes have corresponding kinematic effects and have been interpreted to be due to the specific roles of tactile feedback coming from different areas on the skin of the foot while walking (see Zehr & Stein, 1999, for review).

We recently observed that the pattern of cutaneous reflexes evoked by stimulation of the superficial radial nerve (Zehr & Chua, 2000) during rhythmic arm movement shared some features with the pattern of reflex modulation seen after stimulation of the lower limb analogue of the superficial radial nerve, the superficial peroneal nerve (Zehr *et al.* 1997). The main result from this study was that cutaneous reflexes in some muscles of the upper and lower arm behave differently from what has been shown in the lower limb. Cutaneous reflexes in some muscles studied were linearly related to the background movement-related EMG (Zehr & Chua, 2000) in contrast to the pattern seen in the human lower limb during a rhythmic movement such as walking (Van Wezel *et al.* 1997; Komiyama *et al.* 2000). Some muscles, such as posterior deltoid, biceps brachii and flexor carpi ulnaris, did show phase-dependent modulation such as seen in the lower limb (Zehr & Chua, 2000). The extent to which phase-dependent modulation might be observed in other muscles or after stimulation of other nerves is at present unknown.

Our working hypothesis in these and previous experiments (Zehr & Chua, 2000) has been that the mechanism and observed patterns of reflex modulation are conserved between the human lumbar and cervical spinal cords. If this is the case, control mechanisms and resultant reflex modulation patterns should be similar between the human upper and lower limbs during rhythmic movement. Thus, we hypothesized that task dependency and nerve specificity would be seen when cutaneous reflexes were evoked from three distinct skin areas of the human hand during rhythmic arm movement.

METHODS

Subjects

Eleven subjects who were free from documented neurological disease participated in the experiments with informed, written consent. Subjects ranged in age from 23 to 38 years. 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

As the general experimental methodology is similar to that described previously (Zehr & Chua, 2000), only differences in methodology are highlighted here. Subjects performed rotational arm cranking (~0.6 Hz) on a custom made hydraulic arm ergometer. The crank arms of this ergometer were mounted to two hydraulic pumps that provided an adjustable but constant resistance without the flywheel inertial effects that are seen with a cycle ergometer. As with the previous study, subjects gripped the handgrips firmly but comfortably with the forearms in a pronated position. The resistance could be adjusted with a pressure valve connected in series and was set to provide a liminal resistance to produce muscle activation in the upper limb without leading to excessive fatigue (~170–340 kPa).

Cycle timing

During rotational arm cranking, the position of the ergometer crank arms in the movement cycle was determined from a linear continuous turn potentiometer that was connected in series with the chain and that reset with each movement cycle. The movement cycle is defined here relative to a clock face. Thus, 'top dead centre', or the position when the ipsilateral crank is pointing straight up, is defined as 12 o'clock with positional definitions continuing clockwise (see Fig. 1). All references to position in the movement cycle are thus given with respect to a clock face. Offline, responses occurring at a given position in the movement cycle were partitioned together with reference to these positional definitions. In correspondence with this, the movement cycle was partitioned into 12 separate bins. Accordingly, bin 1 is that part of the movement cycle that covers the excursion from 12 to 1 o'clock, bin 2 from 1 to 2 o'clock, and so on. This is illustrated in Fig. 1.

Nerve stimulation

Nerve stimulation was delivered pseudorandomly (providing stimuli about once every three movement cycles) with a Grass S88 (Grass Instruments, AstroMed Inc.) stimulator connected in series with an SIU5 isolator and a CCU1 constant current unit. The superficial radial (SR) nerve (innervating the dorsal surface of the hand towards the index finger and thumb), the median nerve (innervating the lateral portion of the palmar surface of the hand) and the ulnar nerve (innervating the medial edge of the hand) were stimulated in separate trials. All three nerves were stimulated with trains of 5×1.0 ms pulses at 300 Hz. These nerves were selected as they are the anatomical correlates of three nerves which we have previously studied in the human lower limb (Zehr *et al.* 1997, 1998). That is, SR and superficial peroneal, median and distal tibial, and ulnar and sural nerves are anatomical analogues in the hand and foot, respectively. The electrodes for SR nerve stimulation were placed on the dorsal surface of the forearm just proximal to the radial head and the crease of the wrist joint. The electrodes for median nerve stimulation were placed on the ventral surface of the forearm just proximal to the radial head and those for ulnar nerve stimulation were also on the ventral surface but over the head of the ulna. Stimulation procedures were similar to our other studies of the lower (Zehr *et al.* 1997) and upper (Zehr & Chua, 2000) limbs. Stimulation intensity was set at ~$2 \times$ radiating threshold (RT) for each subject.

The stability of the stimulation throughout the movement cycle was checked at four equidistant positions of the crank cycle with the arms held in static postures. Subjects were initially stimulated at the top of the movement cycle (12 o'clock) and asked to rate the perceived stimulation intensity to be 5 on a scale of 1 to 10. Then, the three other equidistant positions (3, 6 and 9 o'clock) were sampled and subjects were asked to provide a score of intensity relative to the 12 o'clock position. To determine if there were any changes in the perception of subjects during this procedure, the 12 o'clock position was repeated again and the intensity score for this position given as the average value taken over the two presentations. Further, in an attempt to reduce any movement of the stimulating electrodes that could possibly affect stimulus constancy, subjects wore a wrist brace on the stimulated hand. This brace significantly reduced wrist movement amplitude and helped maintain stimulus constancy.

Electromyography

EMG methodology was as described previously (Zehr & Chua, 2000). Muscles studied included first dorsal interosseus (FDI), flexor carpi ulnaris (FCU), extensor carpi ulnaris (ECU), flexor carpi radialis (FCR), biceps brachii (Bic), triceps brachii (Tri), anterior deltoid (AD), and posterior deltoid (PD). The majority of EMG recordings were ipsilateral to the site of nerve stimulation, with the exception that AD and PD were recorded bilaterally. EMG signals were pre-amplified and bandpass filtered at 100–300 Hz (P511 Grass Instruments, AstroMed, Inc.). Offline they were full-waved rectified during the analysis process. This filtering process results in very little

spread of the stimulus artefact and is one which we have previously employed (Zehr *et al.* 1997; Zehr & Chua, 2000).

Data acquisition and analysis

All data were sampled at 1000 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. Averaging throughout the movement cycle was conducted as previously (Zehr & Chua, 2000) with the exception that 12 bins were used in this study. During static contractions, averages of 20 sweeps were collected (Zehr *et al.* 2001).

EMG analysis

Cutaneous reflexes. For each subject, subtracted EMG traces from each muscle were analysed for peak reflex amplitudes at two distinct epochs termed early ($\sim$50–75 ms to peak) and middle ($\sim$75–120 ms to peak) latencies as in our previous paper (Zehr & Chua, 2000). For each subject, cutaneous reflexes within a muscle were normalized to the peak value of the control (unstimulated) EMG for that muscle across the movement cycle.

Background EMG patterns. As described above, control EMG amplitudes were calculated for each position of the movement cycle on the data from trials without stimulation. To determine the extent to which phasic background EMG patterns were observed when using the hydraulic egometer, the modulation index (MI $=$ [(EMG$_{max}$ − EMG$_{min}$)/EMG$_{max}$] × 100) used previously (Zehr & Chua, 2000), was calculated for each muscle throughout the movement cycle.

Statistics

In all instances, analysis was conducted on averaged values for each subject from each position in the movement cycle. Significant reflexes were calculated by comparing the values for control and stimulated positions for each parameter. Analysis of variance was used to determine the main effects and to ascertain significant differences between nerves. Linear regression analysis was used to determine significant relationships between reflex amplitudes and background EMG levels. Descriptive statistics included means ± standard error of the mean (S.E.M.) or standard deviation (S.D.). Statistical significance was set at $P < 0.05$.
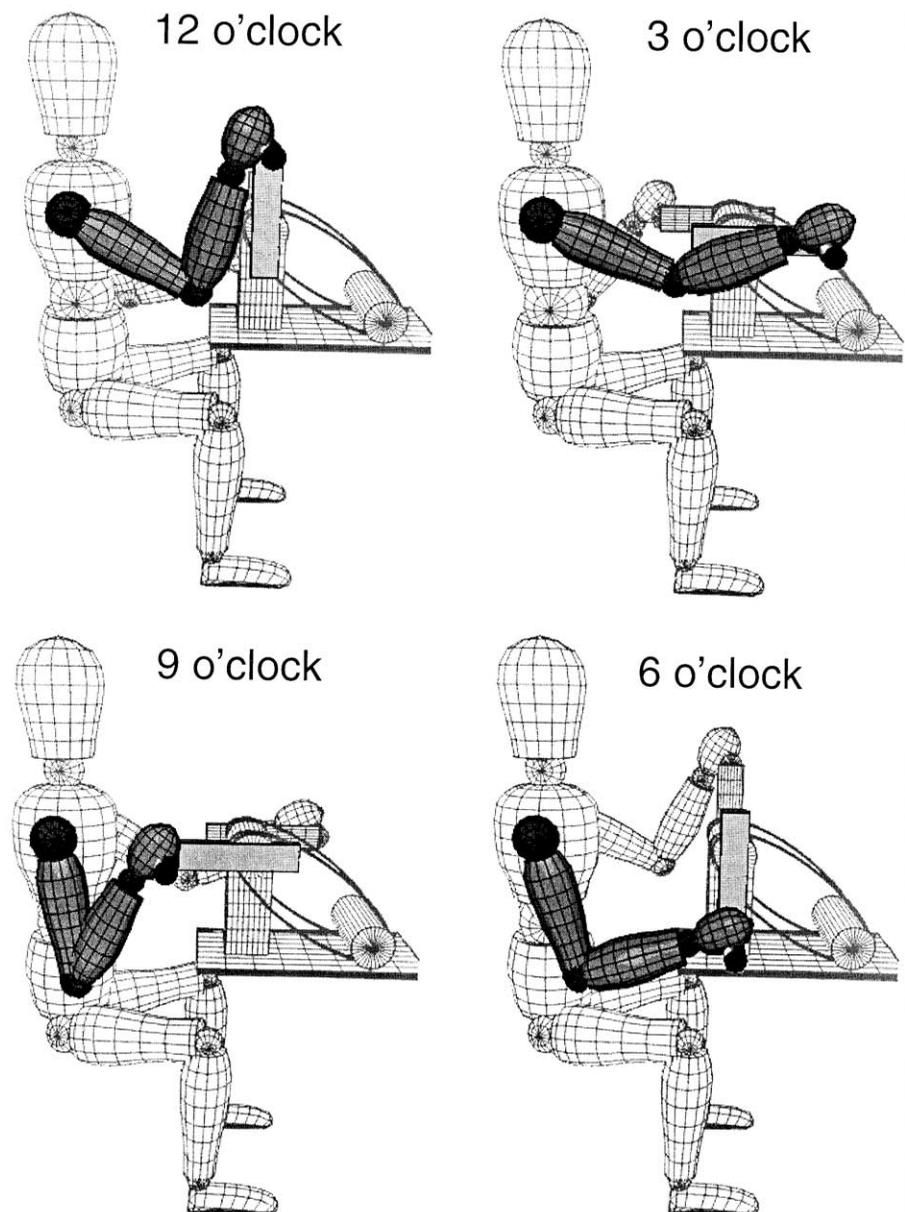

Figure 1. Schematic illustration of the orientation of the upper limb in relation to the crankarm during arm cycling

The figure should be read clockwise from top left and illustrates the 12, 3, 6 and 9 o'clock positions. Note that the orientation of the ipsilateral (stimulated) arm is shown as the darkened limb.
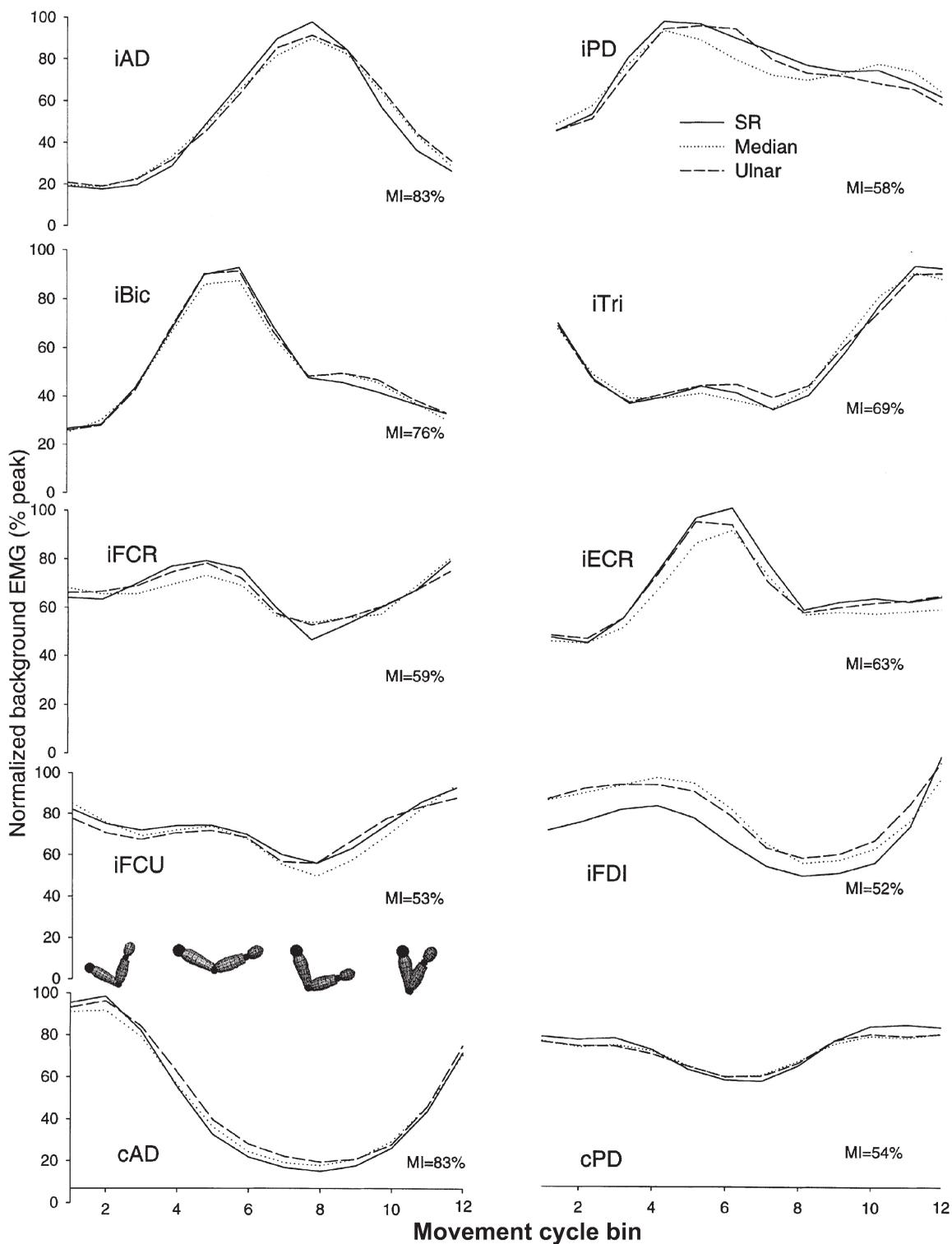
Figure 2. Normalized background EMG during rhythmic arm cycling

Values are averaged across all subjects for each nerve stimulation condition. Abbreviations are: AD, anterior deltoid; PD, posterior deltoid; Bic, biceps brachii; Tri, triceps brachii; FCR, flexor carpi radialis; ECR, extensor carpi radialis; FCU, flexor carpi ulnaris; FDI, first dorsal interosseus; SR, superficial radial nerve. i and c denote ipsilateral and contralateral (relative to site of stimulation) muscles. Shown at bottom right for each muscle is the modulation index (MI) calculated across all three nerve conditions and expressed as a percentage. Values are normalized to the peak value obtained during arm cycling for each subject. The approximate position of the ipsilateral arm in the movement cycle is indicated at the bottom of the iFCU trace. Note that this is a replotting of the ipsilateral arm from Fig. 1.

RESULTS

EMG patterns of arm muscles during rhythmic cyclical movement

Background EMG levels were rhythmically modulated according to the position in the movement cycle ($P < 0.001$). Plotted in Fig. 2 are the mean rhythmic background EMG values normalized to the peak in the movement cycle averaged across all subjects for each of the three nerves stimulated. As a measure of rhythmic activation, an MI was calculated for each muscle for each subject. The overall MI taken across all nerve conditions and across all subjects is shown inserted into the bottom right corner of each panel in Fig. 2. The muscles that had the largest modulation were the shoulder extensors iAD and cAD as well as the elbow flexor iBic and extensor iTri. The muscles acting at the wrist tended to have shallower activation profiles.

Reflex latencies

For reference, latencies to the peak response for the early and middle latency epochs are shown in Table 1 for all combinations of muscle and nerve. There was considerable similarity in the peak latencies for all muscles across the three nerve stimulation conditions.

Reflex modulation patterns across the movement cycle

Examples of reflex traces in iFCU to stimulation of SR, median, and ulnar nerves are shown in Fig. 3. Reflex amplitudes for early (50–75 ms) and middle (75–120 ms; highlighted on Fig. 3) latency epochs were calculated for all nerves and are plotted in Figs 4 and 5, respectively. In both figures, reflexes to stimulation of SR, median and ulnar nerves are shown superimposed for each muscle. To provide a reference for the activation level for each muscle at the time of reflex sampling, traces representing the average control background EMG are also shown as vertical lines.

Statistical analysis revealed a main effect for movement position but no interaction with the nerve stimulated. Early latency reflexes in iAD and cAD ($P < 0.001$), iPD ($P < 0.05$), iTri ($P < 0.001$), iECR ($P < 0.03$) and iFDI ($P < 0.001$) were significantly modulated by position in the movement cycle after stimulation of each of the three nerves (Fig. 4). At middle latency, reflexes in iAD, cAD, iTri and iFDI were significantly (all at $P < 0.001$) modulated by cycle position when collapsed across nerve conditions (main effect for position in cycle; Fig. 5). Thus,
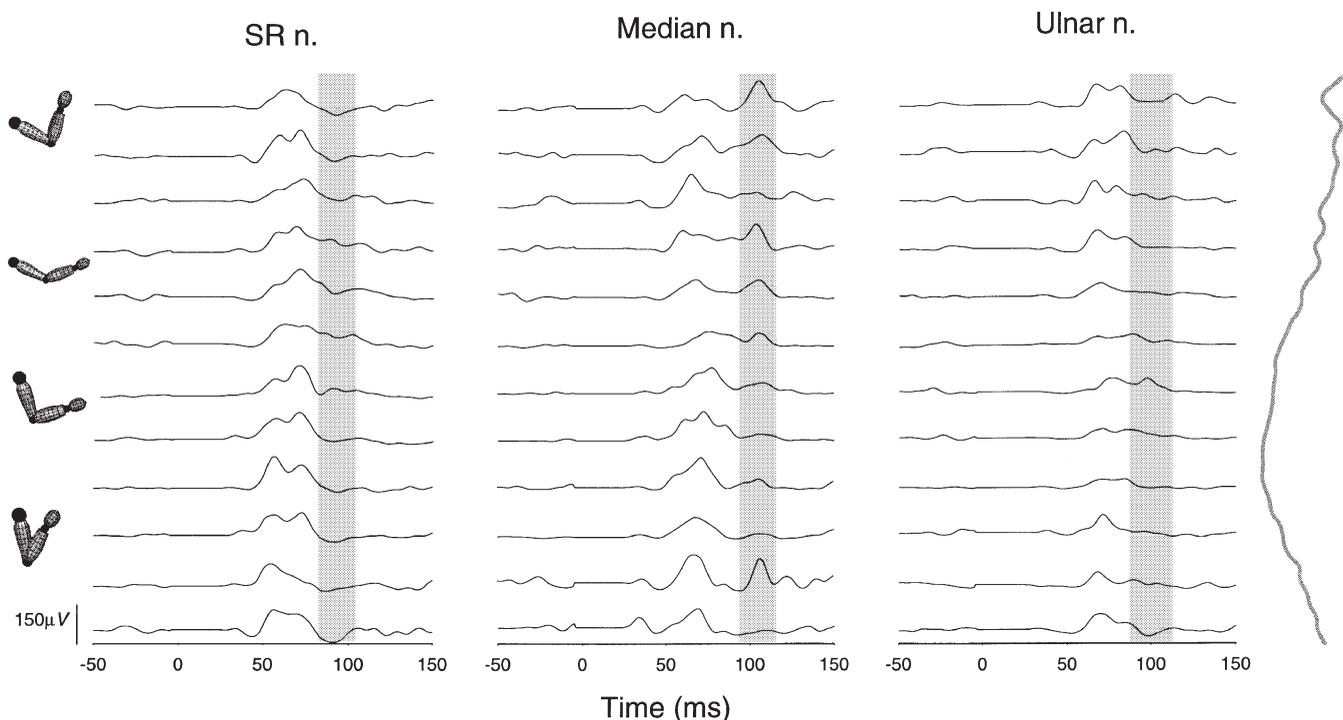

Figure 3. Subtracted reflex EMG traces in iFCU muscle from one subject evoked by SR (superficial radial), median and ulnar nerve stimulation during arm cycling

The grey rectangle highlights the peak response observed during the middle latency window. Note the reversed sign of the middle latency response between SR (suppression) and median nerves (excitation). The cartoon arm on the left indicates position in the movement cycle from 12, 3, 6 and 9 o'clock. The stimulus artifact has been removed from each trace and replaced by a flat line extending from time 0 out to approximately 20 ms post-stimulus. The vertical trace plotted to the right of the figure indicates the approximate background EMG in FCU muscle. Note that large reflexes at early latency (e.g. 50–75 ms post-stimulus) were seen even during periods of low EMG (see 6 o'clock position for all three nerves).

Table 1. Time (ms) to the peak of early and middle latency reflexes

Muscle	SR		Median		Ulnar	
	Early	Middle	Early	Middle	Early	Middle
iAD	70 ± 7	106 ± 12	72 ± 6	106 ± 14	75 ± 6	106 ± 9
iPD	71 ± 6	103 ± 13	74 ± 7	103 ± 14	71 ± 8	100 ± 16
iBic	69 ± 5	106 ± 8	70 ± 5	99 ± 12	74 ± 7	100 ± 4
iTri	64 ± 5	101 ± 13	72 ± 9	109 ± 10	76 ± 10	108 ± 13
iFCR	65 ± 7	103 ± 9	71 ± 7	104 ± 14	71 ± 9	98 ± 15
iECR	69 ± 9	105 ± 16	73 ± 10	109 ± 12	74 ± 8	106 ± 7
iFCU	67 ± 8	105 ± 17	73 ± 4	102 ± 9	75 ± 5	108 ± 3
iFDI	64 ± 8	102 ± 12	68 ± 6	111 ± 12	69 ± 10	104 ± 13
cAD	80 ± 8	114 ± 11	81 ± 4	121 ± 8	82 ± 8	120 ± 6
cPD	81 ± 8	116 ± 7	78 ± 14	104 ± 10	86 ± 5	111 ± 13

Muscles are ipsilateral (i) or contralateral (c) relative to the site of stimulation. AD, anterior deltoid; PD, posterior deltoid; Bic, biceps brachii; Tri, Triceps brachii; ECR, extensor carpi radialis; FCR, flexor carpi radialis; FCU, flexor carpi ulnaris; FDI, first dorsal interosseus; SR, superficial radial. Values are combined from all subjects in all conditions and are means $\pm$ S.D.

Table 2. Correlation coefficients for regression analysis of early and middle latency reflexes and background EMG during arm cycling for all three cutaneous nerves studied

Muscle	SR		Median		Ulnar	
	Early	Middle	Early	Middle	Early	Middle
iAD	$-0.950*$	$0.793*$	$-0.957*$	0.397	$-0.792*$	0.397
iPD	0.115	0.403	0.159	0.330	-0.079	0.270
iBic	$-0.812*$	0.081	0.444	0.478	0.186	$-0.682*$
iTri	$-0.905*$	$0.742*$	$-0.930*$	$0.680*$	$-0.974*$	$0.817*$
iFCR	0.268	-0.530	0.411	$-0.574*$	0.146	-0.326
iECR	$-0.901*$	$-0.717*$	$-0.621*$	0.549	0.020	$-0.878*$
iFCU	-0.293	-0.368	0.068	$-0.586*$	0.379	-0.250
iFDI	$-0.832*$	0.327	$-0.577*$	-0.252	$-0.896*$	-0.234
cAD	$-0.895*$	$0.889*$	$-0.965*$	$0.902*$	$-0.927*$	0.457
cPD	-0.228	-0.188	-0.212	$-0.641*$	0.135	0.252

* Significant Pearson r values at the level of $P < 0.05$. Abbreviations are as in Table 1.

cutaneous reflexes from all three nerves were typically phase modulated by movement position during arm cycling.

This is the first study to report bilateral reflexes in shoulder muscles. It is of interest to note the reciprocal pattern of reflexes in AD evoked by stimulation of all three nerves. That is, during the early (e.g. bins 1 and 2), middle (e.g. bins 7 and 8) and late (e.g. bins 11 and 12) portions of the cycle, responses in iAD (top left of Fig. 4) and cAD (bottom left of Fig. 4) are reciprocal. A similar pattern in the middle latency response is seen in these two muscles (see Fig. 5 top and bottom left).

To evaluate the extent to which reflex amplitude was separated from background EMG amplitude, linear regression was performed on the early and middle latency responses. Listed in Table 2 are the Pearson r values from this analysis. Note that for both early and middle latency responses, comparison of the reflex amplitudes with the rhythmic EMG profiles during arm cycling showed that about one-half (27 of 60 cells when taken across all nerve

conditions) demonstrated a significant correlation (indicated by asterisks in Table 2). Thus, reflex amplitudes in some muscle were phase modulated independent of EMG level and others were in concert with fluctuations in the EMG signal.

To determine the effect that arm cycling movement had on the modulation of the reflexes across the different positions we also evaluated whether reflexes were modulated by position in the cycle during static contraction. This analysis revealed that the background EMG level was significantly ($P < 0.03$) altered by movement position for five muscles. However, in no case was a significant main effect for movement position found for early or middle latency reflexes in any muscle. Thus, there was no phase modulation of cutaneous reflexes by alterations in arm posture during static contraction for any nerve stimulated.

Nerve specificity

Nerve specificity represents the extent to which cutaneous afferents from different nerves make specific
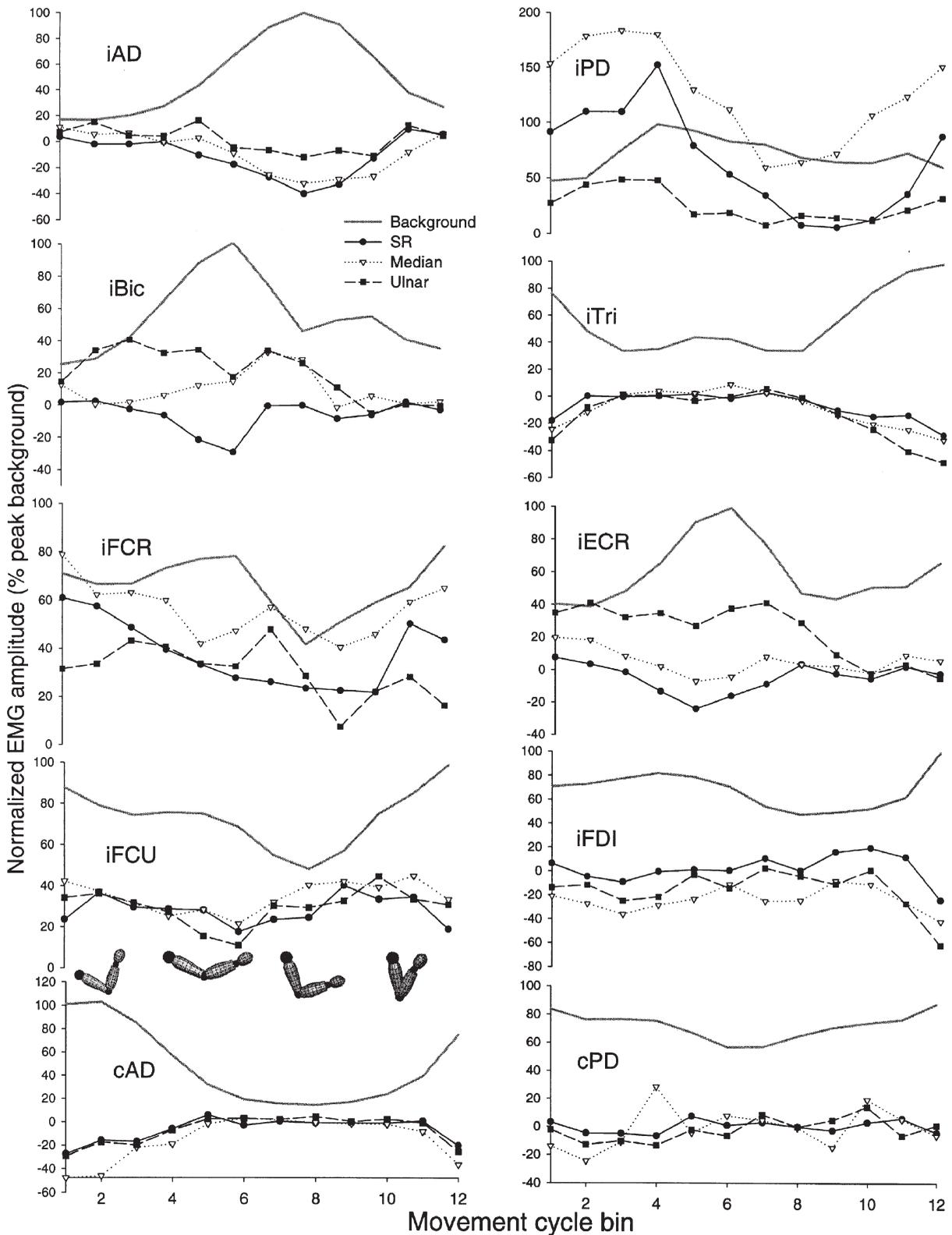
Figure 4. Early latency (50–75 ms post-stimulus) reflexes averaged across all subjects for SR, median and ulnar nerves

Reflex amplitudes have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for each subject and are expressed as percentages. The background EMG trace for each muscle averaged across all conditions is plotted as a continuous line without symbols in each trace. Abbreviations are as in Fig. 2. The approximate position of the arm in the movement cycle is indicated by the cartoon limb at the bottom of the iFCU muscle trace.
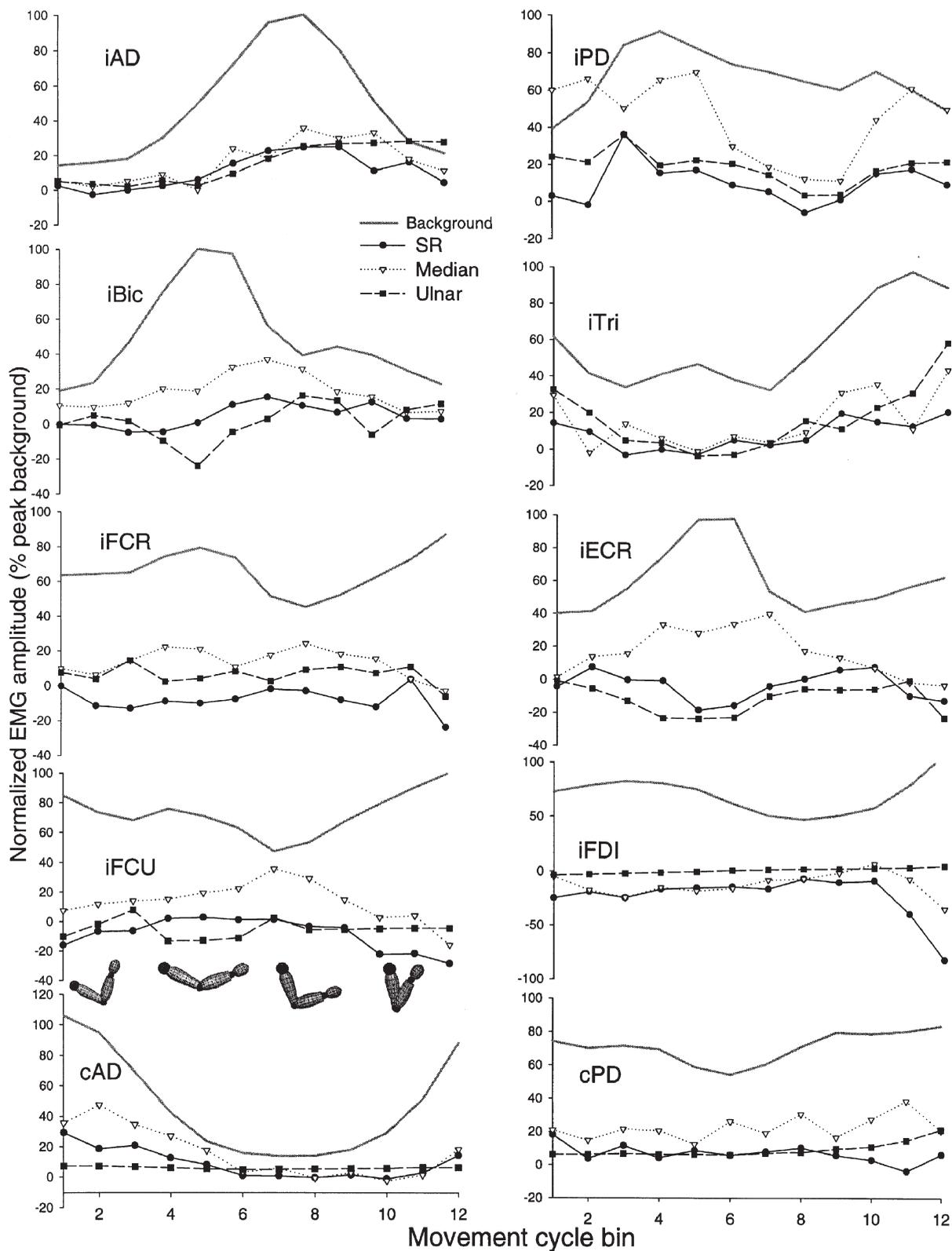
Figure 5. Middle latency (75–120 ms post-stimulus) reflexes averaged across all subjects for SR, median and ulnar nerves

Reflex amplitudes have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for each subject and are expressed as percentages. The background EMG trace for each muscle averaged across all conditions is plotted as a continuous line without symbols in each trace. Abbreviations are as in Fig. 2. The approximate position of the arm in the movement cycle is indicated by the cartoon limb at the bottom of the iFCU muscle trace.

connections with the same muscle. The extent of nerve specificity in this study was evaluated by comparing reflex amplitudes in each muscle. Thus, nerve specificity was indicated by a significant main effect ($P < 0.05$) for nerve in statistical testing of reflex amplitude. Nerve specificity was a common feature at both early and middle latencies, as shown in Table 3 for early latency and Table 4 for middle latency reflexes. To determine if there was a statistically different response between nerves, the row *vs.* column for the nerves in question can
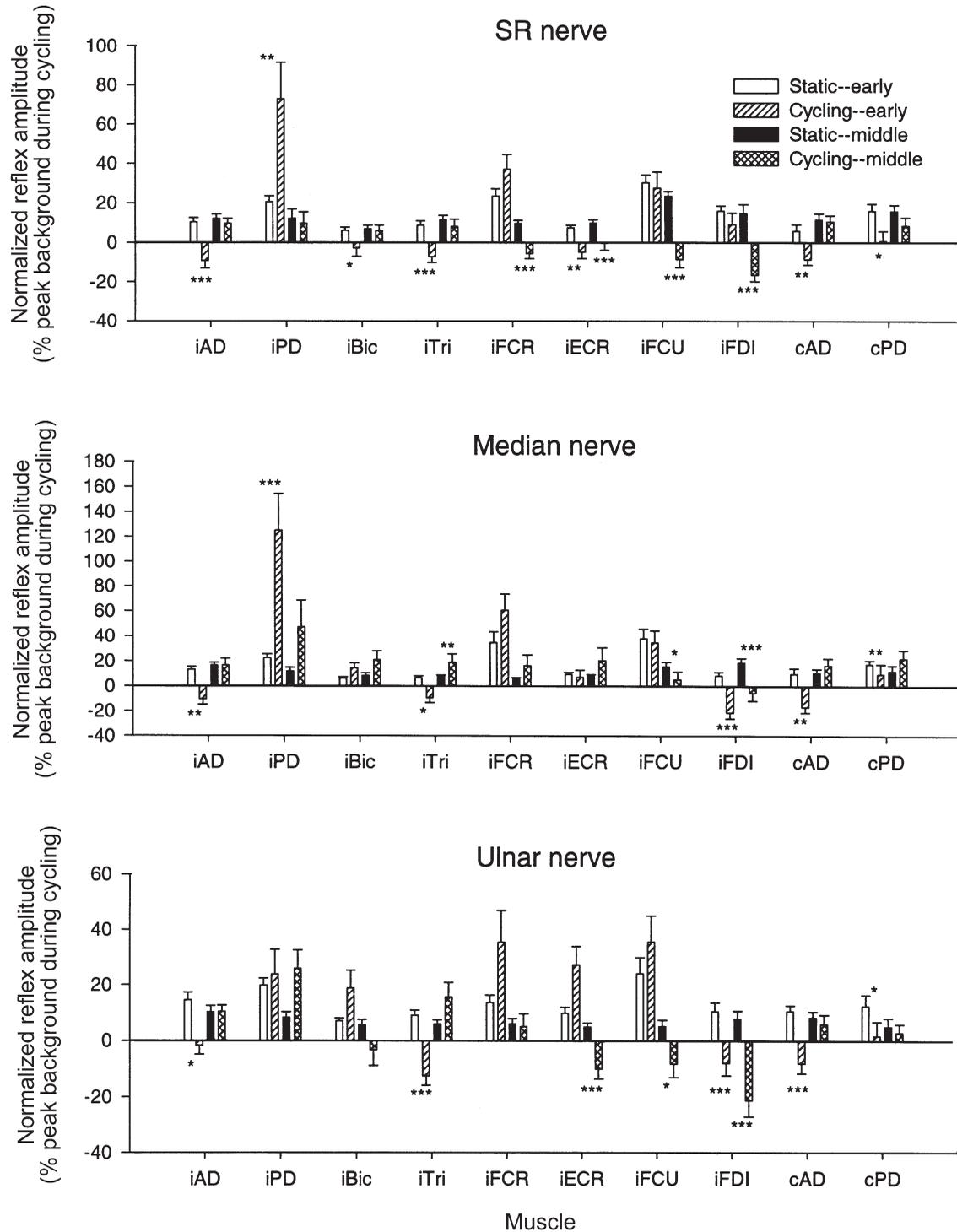

Figure 6. Task-dependent differences in cutaneous reflex amplitude at early and middle latencies during static contraction and cyclical arm movement for each of the three nerve conditions

Values are means for all subjects combined across the common cycling and static contraction positions (i.e. 12, 3, 6 and 9 o'clock positions). Significant differences between static contraction and cycling conditions are indicated as follows: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Abbreviations are as in Fig. 2.

Table 3. Arm muscles that show nerve specificity of cutaneous reflexes at early (50–75 ms) latency

	Ulnar nerve	Median nerve
SR nerve	iAD, iBic, iTri, iECR, iFDI, cAD	iPD, iBic, iECR, iFDI, cAD
Ulnar nerve	—	iAD, iPD, iFCR, iECR, cAD

Differences between the nerves can be obtained by matching rows and columns. In all cases nerve specificity was tested at the level of $P < 0.05$. Abbreviations are as in Table 1.

Table 4. Arm muscles that show nerve specificity of cutaneous reflexes at middle (75–120 ms) latency

	Ulnar nerve	Median nerve
SR nerve	iFCR	iPD, iBic, iFCR, iECR, iFCU, iFDI, cAD, cPD
Ulnar nerve	—	iBic, iECR, iFCU, iFDI, cAD, cPD

Differences between the nerves can be obtained by matching rows and columns. Abbreviations are as indicated in Table 1. In all cases nerve specificity was tested at the level of $P < 0.05$.

be compared. For example early latency reflexes in cAD were significantly different between all three nerves, which is determined by noting that cAD is indicated in the row comparing SR–ulnar, SR–median and ulnar–median in Table 3.
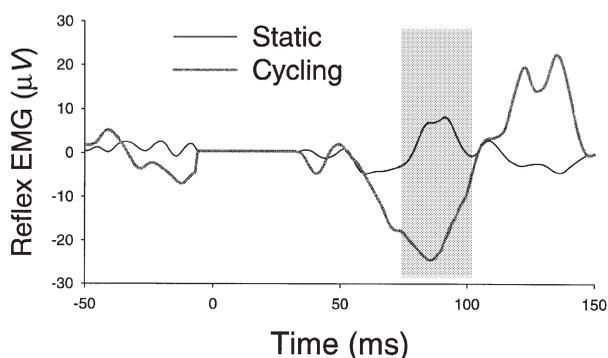
At early latency, the only muscles that did not show nerve specificity were iFCU and cPD, whereas at middle latency, iAD and iTri failed to show nerve specificity. It is notable that a consistent finding was nerve specificity between SR and median nerves that was particularly evident at the middle latency (see Table 4). An example of this can be seen in Fig. 3 by comparing the middle latency responses (highlighted by the grey rectangle) in iFCU muscle evoked by SR (suppression) and median (excitation) nerve stimulation.

The largest nerve specificity can be seen in differences in reflex amplitude observed in iPD, iBic, iFCR and iECR

Figure 7. Task-dependent reflex reversal in the middle latency reflex for one subject

Plotted are subtracted reflex EMG traces for cAD muscle for one subject obtained during static contraction and arm cycling. The middle latency response has been highlighted by the vertical grey rectangle. Note the reversal in sign from excitation during static contraction (thin line) to inhibition during arm cycling (thick line).

(see Fig. 4) at early latency. At middle latency (Fig. 5), the largest differences were seen in iPD, iBic, iFCR, iECR, iFCU and cAD. Responses to median nerve stimulation were typically facilitatory at both early and middle latency, whereas responses to SR and ulnar nerves could be either facilitatory or suppressive at either latency.

Task dependency of cutaneous reflexes

To directly compare static and dynamic reflexes at matched positions, data from the four positions (12, 3, 6 and 9 o'clock) for static contraction and for arm cycling were combined. That is, data from each position for each nerve have been combined to provide values for each latency and movement condition. Plotted in Fig. 6 are early and middle latency responses for static contraction and arm cycling shown for SR (top), median (middle) and ulnar (bottom panel) nerves. For SR nerve reflexes, there was task-dependent modulation (main effect for task; $P < 0.04$–$P < 0.001$) at the early latency in 7 of 10 muscles and at the middle latency in 4 muscles out of 10. For ulnar nerve, five muscles showed task dependency at the early and three at the middle latency. This was seen in six muscles at early and three muscles at middle latency for median nerve stimulation. Thus, a common observation was significant task-dependent modulation of cutaneous reflexes in arm muscles when comparing static contraction with cycling movement. This observation was independent of the stimulated nerve. The task dependency could be observed as a change in reflex amplitude or of reflex sign. Plotted in Fig. 7 is an example of task-dependent reflex reversal in the sign (excitatory during static contraction and inhibitory during movement) of a middle latency SR nerve reflex in cAD muscle for one subject. Generally, cutaneous reflexes were larger during cycling as compared to static contraction (e.g. see iPD after stimulation of all three nerves). In some instances the task dependency was also expressed as a switch in the sign of the cutaneous reflexes from facilitatory during static contraction to inhibitory during movement (e.g. see iFDI and iTri muscles for all three nerves).

Perceived intensity of stimulation

To determine if there was significant mechanical movement of the electrodes overlying the SR, ulnar and median nerves which could lead to stronger or weaker stimulation at different points of the movement cycle, subjective ratings were calculated at four equidistant portions of the cycle (12, 3, 6 and 9 o'clock) during static contraction. Across all nerve stimulation conditions, there were no significant differences in the ratings of perceived intensity at any static arm crank position. Thus, differences in reflexes across the movement cycle were not likely to be due to changes in the intensity of stimulation induced by mechanical movement of the electrodes themselves, but rather to underlying neural control mechanisms regulating reflex transmission during rhythmic movement.

DISCUSSION

This study represents the second in a series of studies investigating and quantifying the control patterns of reflexes observed during rhythmic movements of the human upper limbs. This study also represents our first use of a newly constructed hydraulic ergometer that permits regulation of cyclic movement without extraneous inertial effects. The main observations were that both nerve specificity and task dependency were seen during human upper limb movement. These observations corroborate our previous results on phase modulation of cutaneous reflexes from SR nerve during cyclical arm movement on a modified cycle ergometer (Zehr & Chua, 2000). This is the first documentation of cutaneous reflexes from median and ulnar nerves during rhythmic arm movement and also provides an extension of reflex modulation during rhythmic arm movement to the contralateral upper limb.

Experimental limitations

A key issue to be concerned with in experiments of cutaneous nerve stimulation is stimulus constancy because it is possible that the relative orientation of the stimulating electrodes (on the skin) and the underlying nerve may change with movement. As there is no convenient method available to monitor the actual sensory volley evoked by cutaneous nerve stimulation during movement, we instead must rely on more indirect methods. In this study, an estimate of the stimulus constancy and stability was obtained by having subjects subjectively rate the intensity of stimulation at four different positions during static contraction. There was no significant effect of movement position on the perceived intensity of cutaneous stimulation for all three nerves, as previously reported for the SR nerve alone (Zehr & Chua, 2000). Further, we also used a soft, flexible wrist brace to reduce the likelihood of electrode movement. Therefore, we do not feel that the phase-dependent and task-dependent changes in reflex modulation observed here are due to methodological limitations.

Background EMG patterns

Whilst we previously identified that rhythmic EMG bursting patterns occur in arm muscles during cycling on a flywheel ergometer (Zehr & Chua, 2000), it was possible that cyclical movement performed on a hydraulic ergometer with no inertial effects might have different patterns, such as increased coactivation. However, EMG patterns were quite similar to those documented previously for FDI, FCU, Bic, Tri, iAD and iPD muscles. Additionally, muscles iFCR, iECR, cAD and cPD (previously undocumented) were also phase modulated during rhythmic movement. In examining the phasic activation patterns of the arm muscles shown in this study and taken in concert with our previous observations on a flywheel ergometer (Zehr & Chua, 2000), we are confident that the model we are using to study reflex modulation during rhythmic upper limb movement is valid.

Task modulation of upper limb cutaneous reflexes

In the lower limb, it has been repeatedly demonstrated that reflexes undergo tremendous modulation depending upon the context in which they are evoked (for review see Stein & Capaday, 1988; Zehr & Stein, 1999). There has been much less evidence for task specificity during movement in the human upper limb. When the issue of task specificity has been addressed in the upper limb, it has often been in the context of reflex modulation by change in the type or intent of contraction (e.g. co-contraction) (Aimonetti *et al.* 1999, 2000). Additionally, some evidence also suggests that stretch reflexes in the upper limb may be differentially modulated depending upon the intent of the subjects during a sinusoidal tracking task (Dietz *et al.* 1994). Further, task-dependent changes in cutaneous reflexes of FDI muscle evoked by digital nerve stimulation have also been demonstrated (Evans *et al.* 1989).

The observations reported here, that reflexes evoked by stimulation of the three major cutaneous nerves innervating the hand are task specific between static (always excitatory) and rhythmic movement (larger or inhibitory), are the first such observations in the human upper limb during large amplitude movements of both arms. It had previously been shown in the leg that cutaneous reflexes were of larger amplitude during running when compared to standing (Duysens *et al.* 1993). We later showed that the response to stimulation of the three major cutaneous nerves innervating the foot were all suppressive in the ankle flexor and extensor muscles while standing, in contrast to their variable expression during locomotion (Komiyama *et al.* 2000). The most directly relevant study to the present one concerns cutaneous reflexes which were evoked during leg cycling and static contraction at matched positions (Zehr *et al.* 2001). In this study, we observed that cutaneous reflexes evoked by stimulation of the distal tibial nerve were suppressive during cycling and excitatory during static

contraction. Interestingly, suppressive responses were observed here during arm cycling but not during static contraction (see Fig. 6). Thus, the task-specific responses to cutaneous stimulation during arm cycling observed here are similar to that seen during leg cycling (Zehr *et al.* 2001). This suggests the possibility of similar underlying neural mechanisms.

Nerve specificity in the upper and lower limbs

Nerve specificity, or the production of reflexes of different sign in the same muscles after stimulation of cutaneous nerves innervating different skin areas, was a common outcome in this study (for detail see Tables 3 and 4 and also compare examples in Figs 4 and 5). Indeed it was more common for nerve specificity to be observed (e.g. early and middle latency responses in iECR in Figs 4 and 5) than to be absent (e.g. early latency responses in iFCU and cAD in Fig. 4). Interestingly, indirect evidence for nerve specificity in the upper limb was shown by Cavallari *et al.* (1985). These researchers demonstrated that an interaction between Ib and cutaneous input depended upon the site of stimulation. Group Ib facilitation from wrist extensor onto wrist flexor muscles was increased by cutaneous stimulation applied to the dorsal skin surface of the hand but not by palmar skin stimulation. Thus the actual location of stimulation on the skin was important in the hand as had previously been documented in the leg (Pierrot-Deseilligny *et al.* 1982).

Nerve specificity was previously described as a functionally important feature of cutaneous reflexes in the lower limb. It was observed that stimulation of different cutaneous nerves in the foot evoked differential reflex modulation during human walking (Van Wezel *et al.* 1997; Zehr *et al.* 1997). In the human lower limb, the functional outcome of the nerve specificity is such that activation of afferents innervating mechanoreceptors of the dorsum evokes different reflexes in tibialis anterior muscle than those evoked by activation of afferents innervating the foot sole. This was particularly evident at the middle latency and was often manifested by a complete reversal in reflex sign between different nerves (Van Wezel *et al.* 1997). In the present study, specificity in the arms was a common outcome (for detail see Tables 3 and 4 and also compare examples in Figs 4 and 5) and thus seems to be a general feature of cutaneous reflexes in the upper and lower limbs.

Phase-dependent modulation of cutaneous reflexes?

It has been documented that during rhythmic arm movement cutaneous reflex amplitude (evoked by SR nerve stimulation) mostly covaried with background EMG ('background-dependent modulation'; Zehr & Chua, 2000). This is in contrast to the pattern seen in the lower limb in which there is often a dissociation between reflex amplitude and EMG level (Van Wezel *et al.* 1997; Komiyama *et al.* 2000). In the larger sample of muscles

studied here and when taking into account responses to all three cutaneous nerves, reflexes in more than half of the muscles failed to demonstrate a significant background dependency (10 of 20 for SR and median nerves and 7 of 10 for ulnar nerve; see Table 2). The significance of this observation is at present unclear, but does suggest that the mechanisms of modulation during arm movement may not be as straightforward as previously postulated (Zehr & Chua, 2000).

Co-ordinated patterns of cutaneous reflexes

Co-ordinated patterns of reflexes evoked in different muscles to the same stimulus (i.e. nerve) can be taken as a sign of functional relevance (see for example the co-ordinated leg muscle reflexes to the stumble-like correction evoked by superficial peroneal nerve stimulation; Van Wezel *et al.* 1997; Zehr *et al.* 1997). Interestingly, there was evidence for a functional co-ordination within cutaneous nerves and between antagonist muscles in the upper limb in this paper. At the early latency (see Fig. 4, in particular bin 5), stimulation of SR nerve evoked facilitation in iFCR (wrist flexor) while simultaneously evoking suppression in iECR (wrist extensor). Interestingly, this relationship was not evident at the middle latency (Fig. 5). It has previously been shown that FCR and FCU muscles share, in addition to strong homonymous connectivity, heteronymous Ia facilitation (Chalmers & Bawa, 1997) that could be useful for grasping or hand stabilization (Bawa *et al.* 2000). Taken together with the current observations on cutaneous inputs, this is suggestive of functionally relevant reflex organization in the human forearm that persists across input modalities (e.g. muscle and cutaneous afferents) during movement.

Additionally, there are crossed effects that can be seen when comparing iAD and iPD with cAD and cPD. As shown in Fig. 4, early in the cycle (e.g. bins 1–2) early latency reflexes are facilitatory in iAD while at the same time suppressive in cAD. Further, at similar positions in the movement cycle, early latency reflexes in iPD (facilitatory) are also opposite to the contralateral responses (suppressive in cPD). Thus, there seems to be a co-ordinated pattern of reflexes to cutaneous nerve stimulation during rhythmic upper limb movement.

Mechanisms of modulation?

A continuing debate has concerned the locus of the mechanisms controlling reflex modulation in the lower limb (Brooke *et al.* 1997). Certain features of cutaneous reflex modulation have been suggested to have central pattern-generating (CPG) elements as an underlying mechanism (Duysens & Van de Crommert, 1998; Zehr *et al.* 2001). We recently suggested that the task dependency of cutaneous reflexes when contrasting static contraction with rhythmic cyclical movements of the legs may be ascribed to a CPG (Komiyama *et al.* 2000; Zehr *et al.*

2001). In this paper, the data on task-dependent modulation are quite similar to the observations made previously in the leg (e.g. task-dependent reflex reversal; see Figs 6 and 7). Thus, this could be interpreted as suggestive of CPG influences during rhythmic cyclical human arm movement providing a further parallel with observations in other species such as the cat (Drew & Rossignol, 1987), but this requires further corroboration.

In summary, we suggest that cutaneous reflexes during rhythmic arm movement share many similarities with observations obtained in the human lower limb. That is, there are task-dependency, nerve-specificity and phase-dependency elements in human upper limb cutaneous reflexes evoked during rhythmic muscle activation.

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Corresponding author

E. P. Zehr: Neurophysiology Laboratory, E-435/439 VVC, Faculty of Physical Education and Recreation, University of Alberta, Edmonton, Alberta, Canada T6G 2N9.

Email: pzehr@ualberta.ca