Effect of concentric and eccentric muscle actions on muscle sympathetic nerve activity

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Carrasco, Dario I., Michael D. Delp, and Chester A. Ray. Effect of concentric and eccentric muscle actions on muscle sympathetic nerve activity. J. Appl. Physiol. 86(2): 558–563, 1999.—The purpose of this study was to determine the effects of concentric (Con) and eccentric (Ecc) muscle actions on leg muscle sympathetic nerve activity (MSNA). Two protocols were utilized. In protocol 1, eight subjects performed Con and Ecc arm curls for 2 min, with a resistance representing 50% of one-repetition maximum for Con curls. Heart rate (HR) and mean arterial pressure (MAP) were greater (P < 0.05) during Con than during Ecc curls. Similarly, the MSNA was greater (P < 0.05) during Con than during Ecc curls. In protocol 2, eight different subjects performed Con and Ecc arm curls to fatigue, followed by postexercise muscle ischemia, by using the same resistance as in protocol 1. Endurance time was significantly greater for Ecc than for Con curls. The increase in HR, MAP, and MSNA was greater (P < 0.05) during Con than during Ecc curls. However, when the data were normalized as a function of endurance time, the differences in HR, MAP, and MSNA between Con and Ecc curls were no longer present. HR, MAP, and MSNA responses during postexercise muscle ischemia were similar for Con and Ecc curls. Con curls elicited greater increase (P < 0.05) in blood lactate concentration than did Ecc curls. In summary, Con actions contribute significantly more to the increase in cardiovascular and MSNA responses during brief, submaximal exercise than do Ecc actions. However, when performed to a similar level of effort (i.e., fatigue), Con and Ecc muscle actions elicit similar cardiovascular and MSNA responses. These results indicate that the increase in MSNA during a typical bout of submaximal dynamic exercise is primarily mediated by the muscle metaboreflex, which is stimulated by metabolites produced predominantly during Con muscle action.

autonomic nervous system; central command; dynamic exercise; isotonic contractions; muscle chemoreflex; muscle metaboreflex; muscle mechanoreflex

STUDIES HAVE DEMONSTRATED that muscle sympathetic nerve activity (MSNA) in humans increases during dynamic exercise (22, 27–29). The majority of these studies suggest that the increase in MSNA during dynamic exercise is reflexly mediated by the activation of chemically sensitive muscle afferents (i.e., muscle metaboreflex) located within the contracting muscle (27–29). More recently, however, it has been demonstrated that central neural mechanisms associated with volitional movement (i.e., central command) can also mediate significant increases in MSNA during intense intermittent isometric exercise (30). In addition to these findings, there are some studies suggesting that activation of mechanosensitive muscle afferents may also be involved in the increase in MSNA during exercise (16, 17).

During dynamic exercise, the muscles perform both concentric (Con) and eccentric (Ecc) actions. Whether both types of muscle actions contribute to the increase in MSNA during exercise is not known. We have recently demonstrated lower heart rate (HR) and higher blood flow to the spleen and stomach during eccentrically biased exercise than during concentrically biased exercise, suggesting lower sympathetic outflow (9). It is known that Ecc actions are metabolically less demanding (3–6) and require the recruitment of fewer motor units than do Con actions to perform comparable levels of work (1, 5, 18). These findings suggest that during a bout of dynamic exercise, when both muscle actions are performed with the same workload and for a similar period of time, Ecc actions probably would contribute to a lesser extent to the activation of the muscle metaboreflex and central command, and thereby to the lesser increase in MSNA, than would Con actions. It is possible, however, that the lower activation of the muscle metaboreflex and central command by Ecc actions may be compensated for by a greater activation of the mechanosensitive muscle afferents as a result of the stretching of the muscle (26) and greater development of intramuscular pressure during this type of muscle action (13). To our knowledge, the contribution of Con and Ecc actions to the increase in MSNA during dynamic exercise has not been determined.

Accordingly, the primary purpose of this study is to determine the contribution of Con and Ecc muscle actions to the increase in MSNA during brief and fatiguing dynamic exercise. It is hypothesized that 1) Con actions contribute significantly more to the increase in MSNA during brief, submaximal dynamic exercise than do Ecc actions; and 2) at similar levels of effort (i.e., fatigue), Con and Ecc muscle actions would elicit similar MSNA responses. We also hypothesized that increases in MSNA observed during either Con or Ecc muscle actions would be mediated by the muscle metaboreflex.

METHODS

Subjects

Sixteen healthy subjects (aged 21–36 yr), 13 men and 3 women, participated in the study. Before the study, subjects...
were informed of the time commitment and procedures. All subjects gave a written consent, agreeing to participate in the study. The study was approved by the Human Subjects Committee at the University of Georgia.

Measurements

Multifiber recordings of MSNA were made with a tungsten microelectrode inserted in the peroneal nerve at the head of the fibula of a resting leg. A reference electrode was placed subcutaneously, 2–3 cm from the recording electrode. Adjustment of the recording electrode was made until sites were found in which clear, spontaneously occurring sympathetic bursts were recorded. The criteria for acceptable recordings of MSNA were as follows: 1) weak electrical stimulation through the electrode elicited involuntary muscle contraction of the appropriate muscle but not paresthesia; 2) tapping or stretching of muscle or tendons innervated by the impaled fascicle evoked afferent mechanoreceptors discharges, but afferent activity was not elicited by stroking the skin; 3) spontaneous pulse-synchronous bursts of sympathetic impulses did occur intermittently and increased during apnea; and 4) a sudden arousal stimulus (yell or clap) did not elicit an increase in sympathetic nerve activity (15). The nerve signal was amplified (20,000–50,000 times), filtered with a bandwidth of 700–2,000 Hz, and passed through a resistance-capacitance integrating network with a time constant of 0.1 s, to obtain a mean-voltage display of the nerve activity. The mean-voltage neurogram was displayed together with the arterial pressure and respiratory pattern on a chart recorder (Gould 2400s) at a paper speed of 5 mm/s and an on-line computer. The nerve traffic was routed to a loudspeaker for monitoring during the study.

Sympathetic bursts were identified by inspection of the integrated-voltage neurogram. Individual burst amplitudes were measured, and MSNA was expressed both in terms of burst frequency (bursts/min or bursts/30 s) and of total MSNA (calculated as the sum of the burst amplitudes and expressed as arbitrary units).

HR was continuously measured using a Biotach monitoring device, and continuous measurements of arterial pressure were made using a Finapres blood-pressure-monitoring device (Ohmeda, Englewood CO). To ensure that subjects avoidedValsalva maneuver during exercise, respiratory patterns were continuously monitored with the aid of a pneumotrace strapped around the chest. During all exercise trials, a venous blood sample, drawn at rest and at the end of 3 min of recovery through a catheter inserted in the brachial vein of the nonexercising arm, was used for determination of blood lactate by using a Yellow Springs Instruments analyzer (model 27; Yellow Springs, OH). At the end of each exercise trial, the ratings of perceived effort (RPE) were determined by the 15-point Borg scale (7) and used as an index of central command activation (10).

Mode of Exercise

All subjects were tested in the sitting position. Concentric muscle actions were performed by raising the dumbbell from the fully extended to the fully flexed position of the forearm (i.e., Con curls). Eccentric muscle actions were performed by lowering a dumbbell from the fully flexed position to the fully extended position of the forearm (i.e., Ecc curls). A metronome was set at 1 pulse/s to aid the subject in maintaining the frequency of the arm curls. The duration of each arm curl lasted 3 s and was followed by a 2-s period in which the arm and the dumbbell were passively returned to the starting position by an investigator (~12 curls/min). MSNA was recorded from the contralateral leg.

Experimental Protocols

Before the first experimental session, the subject's one-repetition maximum (1-RM) was determined for unilateral Con curls. The results of 1-RM test were used to determine the resistance used during the experiment. Additionally, each subject was familiarized with the testing protocols.

Protocol 1. After a 3-min rest period to collect baseline data, Con or Ecc unilateral arm curls were performed for 2 min by using a workload representing 50% of their 1-RM for Con curls. The exercise was followed by a 3-min recovery period. After a 30-min rest period, the subject repeated the same protocol but with the other mode of arm curls. The order of the arm curl was counterbalanced between subjects.

Protocol 2. After a 3-min resting period to collect baseline data, Con or Ecc unilateral curls were performed until fatigue by using a resistance representing 50% of their 1-RM for Con curls. Five seconds before the end of exercise, the circulation to the working muscles was occluded by inflating a pneumatic cuff around the working arm to suprasystolic levels (240 mmHg). Postexercise muscle ischemia (PEMI) was maintained for 2 min and was followed by a 3-min recovery period. After 45 min of rest, the subjects repeated the same protocol by using the other mode of arm curls. The order of the arm curls was counterbalanced between subjects.

Data Analysis

The statistical analysis of the data was performed by using a two-within factors (time and mode of exercise), repeated-measures ANOVA and regression analysis. The Bonferroni method was used for multiple comparisons. A significance level of $P < 0.05$ was used for all tests. Because of the difference in the performance time between Con and Ecc arm curls in protocol 2, the responses were normalized as a function of endurance time (i.e., 25, 50, 75, and 100%). Linear regression was used to compare slopes (i.e., the rate of change) of the variables in protocol 2.

RESULTS

Protocol 1

Responses to Con and Ecc curls during 2 min of submaximal exercise are presented in Fig. 1. HR and mean arterial pressure (MAP) increased significantly during exercise. However, HR and MAP were greater during Con than during Ecc curls. MSNA was similar for Con and Ecc curls at rest (20 ± 4 vs. 19 ± 3 bursts/min, respectively). MSNA expressed as burst frequency did not change during Ecc exercise but was significantly elevated by the second minute of Con exercise. When examined as a percent change of total MSNA, both arm curls elicited a significant increase in MSNA by the second minute of exercise. However, the increase in total MSNA during the second minute of exercise was significantly greater for Con (80 ± 24%) than for Ecc (38 ± 24%) curls. An original recording of MSNA at baseline and during Ecc and Con exercise from one subject is shown in Fig. 2.

Blood lactate concentrations were 1.6 ± 0.2 and 1.7 ± 0.2 mmol/l before Con and Ecc exercise, respectively. Blood lactate increased to 2.4 ± 0.3 and 2.0 ± 0.3
mmol/l after Con and Ecc curls, respectively. The increase in blood lactate concentration was significantly greater for Con than for Ecc curls. RPE were significantly greater after Con (16 ± 1) than after Ecc (13 ± 0) curls.

Protocol 2

Endurance time (i.e., time to fatigue) was significantly greater for Ecc than for Con curls (5.7 ± 0.7 vs. 2.0 ± 0.2 min, respectively). Responses to fatiguing Con and Ecc curls are presented in Figs. 3 and 4. Both modes of exercise produced significant increases in HR and MAP. HR increased progressively throughout the duration of both modes of exercise. The rate of increase in HR was significantly greater for Con than for Ecc exercise (slopes = 15 and 5, respectively). However, when normalized as a percent of endurance time, the increase in HR was similar for Con and Ecc exercise (slopes = 0.3 for both trials) (Fig. 3). HR responses attained similar levels at the end of Con and Ecc curls (115 ± 9 and 109 ± 5 beats/min, respectively). During PEMI, HR responses returned to baseline following both modes of arm curls. MAP increased progressively throughout the duration of Con curls but only during the first half of Ecc curls (Fig. 3). When examined relative to endurance time (Fig. 3), MAP at 25% (108 ± 3 vs. 121 ± 7 mmHg) and 50% (120 ± 5 vs. 128 ± 8 mmHg) was significantly less for Con than for Ecc curls, respectively. However, at 75%, during fatigue and PEMI, MAP responses were similar for Con and Ecc exercise, respectively.

Resting MSNA (bursts/30 s) was similar for Con and Ecc curls (11 ± 2 vs. 10 ± 2 bursts/30 s, respectively) (Fig. 4). MSNA increased linearly during both modes of arm curls. The rate of increase in burst frequency was significantly greater during Con than during Ecc curls (slopes = 5 and 2, respectively). However, when examined at the same relative endurance time, the differences in the rate of increase in MSNA between Con and Ecc actions were no longer present (slopes = 0.1 for both trials; Fig. 4). MSNA responses at 25% (13 ± 3 vs. 13 ± 2 bursts/30 s), 50% (14 ± 2 vs. 16 ± 2 bursts/30 s), and 75% (18 ± 2 vs. 17 ± 2 bursts/30 s) of time to fatigue; at fatigue (20 ± 2 vs. 19 ± 1 bursts/30 s); and during PEMI (21 ± 3 vs. 21 ± 3 bursts/30 s) were similar for Con and Ecc curls, respectively. MSNA

Baseline

Exercise

Baseline

Concentric

Eccentric

Fig. 1. Heart rate (HR), mean arterial pressure (MAP), and muscle sympathetic nerve activity (MSNA) for concentric and eccentric muscle actions during baseline, representing average value over 3 min, during 2 min of exercise, and in 3rd min of recovery. Values are means ± SE. *P < 0.05 vs. baseline; †P < 0.05 vs. eccentric.

Fig. 2. Original tracing of MSNA during eccentric and concentric actions during baseline and in the final 30 s of exercise from 1 subject.
remained significantly elevated during PEMI following both types of arm curls. When examined as total MSNA, sympathetic responses followed the same pattern as burst frequency.

Blood lactate concentrations were 1.6 ± 0.2 and 2.0 ± 0.2 mmol/l before Con and Ecc curls, respectively. Blood lactate concentration was significantly increased (Δ) after Con but not after Ecc curls (Δ0.9 ± 0.2 vs. Δ0.2 ±...
Several investigators have shown that Ecc muscle actions are metabolically less demanding than are Con actions (3–6) and recruit fewer motor units than Con actions when comparable levels of work are performed (1, 5, 18). MSNA during dynamic exercise is thought to be regulated primarily by reflexes arising from the activation of metabosensitive afferent fibers located within the exercising muscle (27–29). Recent human (16, 17) and animal (2) studies have also suggested that mechanosensitive muscle afferents may play a role in this response. Similarly, central neural mechanisms during intense volitional effort have also been thought to contribute (30). Because of the lower metabolic stress and activation of fewer motor units, it would be expected for MSNA to be lower during Ecc than during Con arm curls. However, it is possible that MSNA may increase significantly during Ecc actions as a result of a greater activation of mechanosensitive muscle afferent fibers produced by the stretch of the muscle fibers and the greater intramuscular pressure elicited by these types of muscle actions. Our results support the former rationale. Briefly, submaximal Con arm curls elicited significantly greater MSNA responses than did Ecc curls. Several observations suggest that the greater MSNA during brief, submaximal Con arm curls was mediated by the activation of the muscle metaboreflex and not by central command or activation of the muscle mechanoreflex. First, MSNA did not increase during the first minute of Con exercise but was significantly elevated by the second minute of Con exercise. This time delay between the onset of exercise and the increase in MSNA has been associated with the time needed to change the chemical milieu of the exercising muscle to activate the muscle metaboreflex (15, 20).

Second, the increase in blood lactate concentration was significantly greater during Ecc than during Con actions. However, it is possible that MSNA may increase during Ecc actions as a result of a greater activation of mechanosensitive muscle afferent fibers produced by the stretch of the muscle fibers and the greater intramuscular pressure elicited by these types of muscle actions. Our results support the former rationale. Briefly, submaximal Con arm curls elicited significantly greater MSNA responses than did Ecc curls. Several observations suggest that the greater MSNA during brief, submaximal Con arm curls was mediated by the activation of the muscle metaboreflex and not by central command or activation of the muscle mechanoreflex. First, MSNA did not increase during the first minute of Con exercise but was significantly elevated by the second minute of Con exercise. This time delay between the onset of exercise and the increase in MSNA has been associated with the time needed to change the chemical milieu of the exercising muscle to activate the muscle metaboreflex (15, 20).

Second, the increase in blood lactate concentration was significantly greater during Con than during Ecc exercise. This is consistent with the greater metabolic stress reported by others after Con exercise (3, 6, 14, 19). The greater RPE during Con than Ecc arm curls during protocol 1 may suggest that central command contributed to the greater MSNA response during Con exercise. However, increases in MSNA are thought to be mediated by central command only during intense exercise (30). This was not the case during the 2-min submaximal protocol based on RPE being only 16 and 13 for Con and Ecc exercise, respectively.

The greater increase in MSNA during nonfatiguing Con vs. Ecc arm curls is consistent with our findings of higher HR and lower blood flows to the spleen and stomach during level vs. downhill walking, an eccentrically biased locomotion (9). As discussed earlier, Ecc muscle actions are known to be metabolically less demanding and to develop greater forces than Con muscle actions. Thus it is possible that the brief exercise did not allow the muscle metaboreflex to become fully activated and for muscle fatigue to develop significantly during Ecc actions. To test this hypothesis, Con and Ecc actions were performed to fatigue. Fatiguing Ecc curls not only elicited similar MSNA responses as did Con curls but these responses were maintained during PEMI, suggesting that they were mediated by the muscle metaboreflex. If the muscle mechanoreflex contributed to the increase in MSNA during Ecc or Con arm curls, MSNA would have been expected to increase at the onset of exercise and to decrease during PEMI, when muscle force development had stopped. However, neither of these responses occurred. Still, it is possible that mechanosensitive muscle afferents may have contributed to the increase in MSNA later in the exercise protocol by sensitization of these afferents by increase metabolite production (21, 23).

The increase in blood lactate concentration, although small, was significantly greater for Con than Ecc curls. Small differences in blood lactate concentration have been shown to significantly alter MSNA responses during fatiguing isometric exercise. Ettinger et al. (11), using dichloroacetate, a drug that decreases the formation of lactic acid, reduced blood lactate concentration after fatiguing handgrip by 0.7 mmol/l. This small decrease in lactate was associated with a 51% decrease in MSNA. However, the fact that MSNA responses were increased during Ecc curls at fatigue without a significant increase in blood lactate suggests that the activation of the muscle metaboreflex, and thus of MSNA, is not necessarily associated with blood lactate responses following fatiguing dynamic exercise. This finding agrees with the report of Sinoway and colleagues (24), who found that the activation of the muscle metaboreflex during fatiguing, rhythmic, isometric handgrip exercise was not related to the intracellular hydrogen ion concentration. Several other metabolic substances known to be released during muscle contraction, such as diprotonated phosphate (25), adenosine (8), and derivatives of arachidonic acid (12), have also been related to the activation of this pressor reflex and to the increase in MSNA during exercise. The increase in MSNA during Con and Ecc actions may possibly be mediated by the action of one or more of these metabolites or by a currently unknown metabolite.

Recently, central command has been demonstrated to play a significant role in the activation of MSNA during intense intermittent isometric muscle contractions in humans (30). In this study (30), a synchronization of MSNA to that of motor activity was demonstrated, such that MSNA during intense, repetitive isometric exercise was significantly elevated during the contraction compared with the relaxation periods. Such synchronization was not observed in the present study. The difference of the exercise intensities utilized could be one reason for the discrepancy between the studies. In the study of Victor et al. (30), the contribution of the central command to the regulation of MSNA was observed only at the highest intensity of the exercise (75% maximal voluntary contraction (MVC)) but not during mild or moderate intensities of intermittent isometric handgrip (25 and 50% MVC, respectively). However, the fact that after curare a similar synchroni-
zation between MSNA and motor activity was observed, despite a fall in force output below 25% of the initial MVC, suggests that it is the perception of effort and not the actual force output what mediates the activation of central command and the increases in MSNA. Although the exercise intensity in the present study was only 50% of 1-RM for Con curls, the RPE were near maximal (very, very hard) for both muscle actions at fatigue. Based on these findings, it is likely that central command was maximally activated at the end of both fatigueing arm curls.

In summary, the results from the present study demonstrated that brief submaximal Con muscle actions elicit greater cardiovascular and MSNA responses than do Ecc muscle actions. However, when performed to a similar level of effort (e.g., fatigue), Con and Ecc arm curls elicit similar cardiovascular and MSNA responses. These results indicate that the increase in MSNA during a typical bout of submaximal dynamic exercise is primarily mediated by the muscle metaboreflex that is stimulated by metabolites produced predominantly during Con muscle action.

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