J. Physiol. (1972), 226, *pp.* 173–190
With 8 *text-figures*
Printed in Great Britain

CARDIOVASCULAR AND RESPIRATORY RESPONSES TO CHANGES IN CENTRAL COMMAND DURING ISOMETRIC EXERCISE AT CONSTANT MUSCLE TENSION

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(*Received 30 March 1972*)

SUMMARY

1. Experiments were designed to show whether elements of the command descending from higher centres to exercising muscles provide an input for cardiovascular and respiratory control. Vibration, known to be a powerful stimulus to the primary afferents from muscle spindles, was applied to the biceps tendon of human subjects performing sustained isometric contractions with the biceps or the triceps muscle. When the biceps was contracting this activation of muscle spindle primary afferents in it provided an element of reflex excitation, so that less central command was required to achieve a given tension. When triceps was contracting, the activation of muscle spindle primary afferents in its antagonist, biceps, contributed an element of reflex inhibition, so that more central command than normally was required to achieve a given tension. The cardiovascular and respiratory responses to an isometric effort could thus be investigated at any tension when the central command was normal, decreased, or increased.

2. Blood pressure, heart rate, and pulmonary ventilation all increase in an isometric effort. The increase in each is less when the central command is reduced. The increase in each is greater when the central command is increased.

3. It is concluded that there is irradiation of cardiovascular and respiratory control centres by the descending central command during voluntary muscular contractions in man.

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INTRODUCTION

Reflexes from contracting muscle are known to affect the cardiovascular and respiratory systems during exercise (Kao & Ray, 1954; Coote, Hilton & Perez-Gonzalez, 1971; McCloskey & Mitchell, 1972). It has not been established whether, in addition, there are effects dependent upon central 'irradiation' (Krogh & Lindhard, 1913), that is, whether the central command descending from higher centres to the exercising muscles provides an input for the cardiovascular and respiratory control.

In the present study a method was used to vary the central command required for a particular muscular action, in this case prolonged isometric contraction of the biceps or triceps muscles of the arm. The tension actually achieved was constant, so that reflex effects from the working muscle should then remain similar whereas responses dependent upon central 'irradiation' would vary. These experiments show that blood pressure, heart rate, and pulmonary ventilation all change with the level of central command.

A brief report of this work has been published previously (Goodwin, McCloskey & Mitchell, 1971).

METHODS

Principle. A subject was asked to hold a constant tension, which was never more than half the tension of his maximal voluntary contraction, with either the biceps or triceps muscle of the arm. The subject was shown a display of the tension he was achieving, which he was asked to align with a marker of required tension. His isometric effort always led to increases in arterial blood pressure and heart rate (Lind, McNicol & Donald, 1966), and ventilation (Wiley & Lind, 1971; Myhre & Andersen, 1971). These changes were compared with those which occurred when the same tension was held by the same muscle for the same time while the central command required to produce the tension was different.

If a small physiotherapy vibrator (Vibratory Massager, Pifco Ltd) oscillating at 100 Hz is applied to the tendon of either the exercising muscle or its antagonist, the central command required to produce a constant tension may be altered. Vibration is known to be a powerful stimulus to muscle spindle primary endings, and can be used, for example, to elicit reflexly a tension in the muscle without central command (De Gail, Lance & Neilson, 1966; Hagbarth & Eklund, 1966). This tension in most subjects was small, being about 10 % of the maximum of which the subject was capable. Because the cardiovascular and respiratory responses to isometric exercise are best seen at tensions of more than 10 % of the maximum (Lind *et al.* 1966) it was more satisfactory to add an element of voluntary contraction to a reflex contraction. That is, a subject would be asked to produce a tension of, say 30 % of his maximal voluntary contraction, but the applied vibration would allow some of this to be achieved reflexly, so that he would require a central command equivalent only to about 20 % of his maximum. A diagram of this principle is shown in Fig. 1.

Alternatively, vibration of an antagonistic muscle will produce disynaptic inhibition of the motoneurones of the active muscle and a greater central command will be required for any muscle tension. In our experiments a subject was asked to produce a given tension with triceps while vibration of biceps, by activating the primary afferents of muscle spindles there, would contribute a reflex inhibition to the motoneurones of triceps. This meant that it was necessary for the subject to call forth a greater central command to achieve the required tension. A diagram of this principle is shown in Fig. 2. The reflex inhibition is not accompanied by detectable contraction of the vibrated antagonist. It is not surprising that the vibrated biceps did not contract, for its motoneurones were presumably being inhibited by elements of the descending command and by spinal reflexes from the contracting triceps. The most satisfactory indicator of contraction here was found to be simple manual palpation of the vibrated antagonist: in random blind trials on our subjects it was found that contractions of 2 % of the maximum could be reliably detected by this method. No contraction of the vibrated antagonist was found in these experiments. Also no evidence of contraction of the vibrated antagonist could be demonstrated by electromyography, although this proved a less sensitive method because of interference caused by vibration.

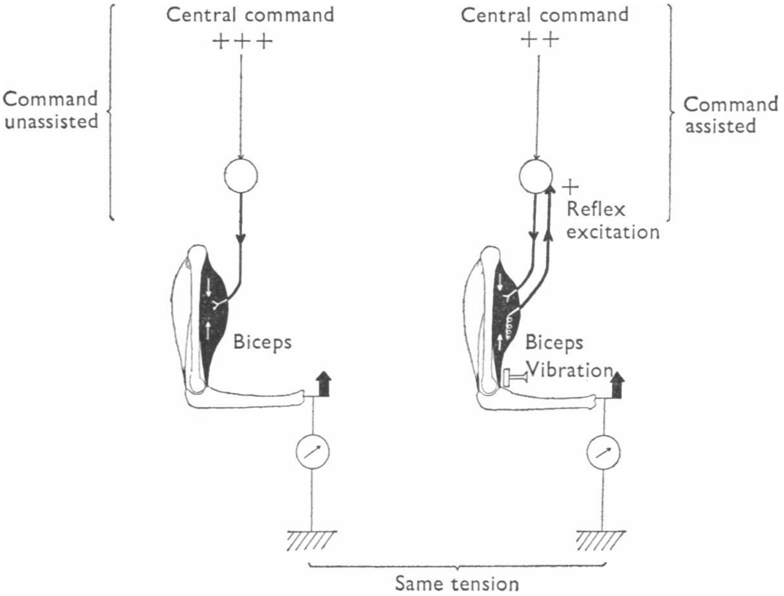

Fig. 1. Principle of an experiment designed to reduce the central command required to achieve a muscle tension. On the left is shown the situation that exists when an upward force is exerted by the forearm through the voluntary contraction of the biceps muscle: the magnitude of the central command required is given as + + +. On the right is shown how vibration is used to excite the primary afferents from muscle spindles of the contracting muscle, thereby contributing an element of reflex excitation to the motoneurones innervating the muscle: the same upward force can thus be exerted by a contraction of biceps which achieves the same tension while requiring less central command (now given as + +).

Evidence that the assisting and inhibiting manoeuvres were working as described was found in the responses seen when vibration was suddenly removed. It was usual in all our vibration experiments, at the conclusion of the period of contraction, to remove the vibrator after first covering up the tension record on the oscilloscope and instructing the subject to 'continue pushing (or pulling) just as hard'. When this was done, the tension achieved fell when the vibration had been assisting the contraction, and rose when the vibration had been inhibiting the contraction. These changes in tension were usually short-lived because the subjects quickly detected the undershoot or overshoot from changes in the pressure exerted by the wrist on the strain gauge, and corrected for them. Fig. 3 shows the typical behaviour in records obtained during the experiments illustrated in Figs. 5 and 7.

Subjects. Experiments were done on fifteen healthy male volunteers aged from 20 to 30 yr. Five of these subjects were judged unsatisfactory because of large variations in their measured parameters at rest or in response to minor extraneous events (e.g. movement of an experimenter in their sight, noises outside the room etc), or because they expressed a particular dislike of the tasks required of them. Results obtained on these subjects will not be presented here. Of the remainder, three were familiar with the aims of the study at the time of the experiments, and seven were not (non-medical volunteers, technicians, or medical students). Several satisfactory subjects were used on more than one occasion.

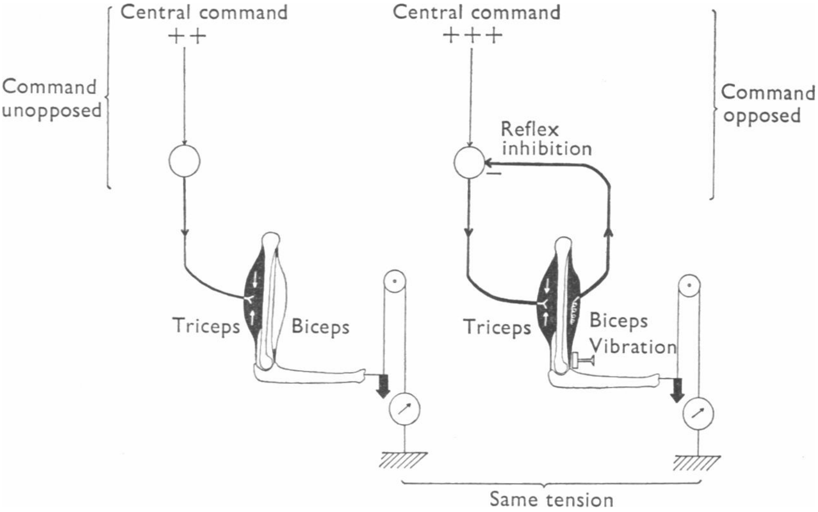

Fig. 2. Principle of an experiment designed to increase the central command required to achieve a muscle tension. On the left is shown the situation that exists when a downward force is exerted by the forearm through the voluntary contraction of the triceps muscle: the magnitude of the central command required is given as + +. On the right is shown how vibration of the biceps, an antagonist of the contracting muscle, is used to excite the primary afferents from muscle spindles in biceps. This contributes an element of reflex inhibition to the motoneurones innervating the contracting triceps. The same downward force can thus be exerted by a contraction of triceps, only if a greater central command (here + + +) is given. The vibrated biceps does not contract during an effort with triceps.

In parallel experiments done with intra-arterial blood pressure recording, two subjects and one of the authors (D.I.M.) were studied.

Experimental procedures. Subjects were seated in a comfortable arm-chair, with their elbows resting on the padded arms of the chair, and their forearms projecting beyond the ends of the arm supports. Isometric contractions of the biceps or triceps of the right arm were usually investigated. For these the right wrist passed through a strong webbing sling attached to a wire cable which connected to a strain gauge fixed to the floor. During biceps contractions the wrist pulled upwards directly from the strain gauge; during triceps contractions, the wire cable from the strain gauge was passed over a pulley fixed to a firm frame above the subject's wrist, so that

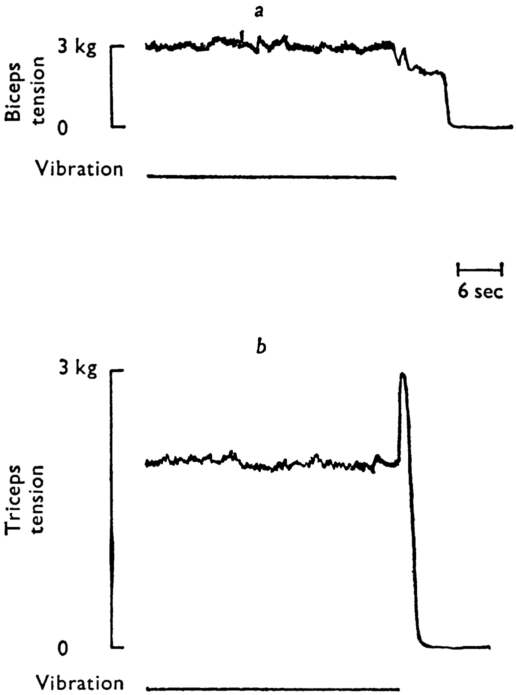

Fig. 3. The effects of removal of vibration during contractions in which vibration was being used to contribute reflex assistance or inhibition. In *a*, a subject was performing the experiment illustrated in Fig. 5, an effort with biceps in which vibration was supplying reflex assistance: removal of vibration led to a fall in achieved tension, presumably to the level appropriate to the reduced central command he was using. In *b*, a subject was performing one of the experiments illustrated in Fig. 7, an effort with triceps in which vibration of biceps was supplying reflex inhibition: removal of vibration led to a rise in achieved tension, presumably to the level appropriate to the increased central command he was using. In each case the subject was told to relax as soon as the extent of the undershoot or overshoot was determined.

downwards pressure of the wrist again registered a tension through the strain gauge. For either type of contraction the wrist was rotated so that the plane of the hand was vertical, and the sling always met the wrist at the same distance from the elbow. Similarly the point of the elbow of the exercising arm was always in the same position on the arm support. The angle at the elbow for any subject in any one study was thus always constant (usually this angle was between 90 and 120°).

Subjects were instructed to confine their efforts in any experiment to the biceps or triceps muscle being tested, and were specifically instructed to avoid using shoulder or trunk movements to alter their leverage. In many experiments the subjects were firmly strapped into the arm-chair with a belt diagonally crossing the right shoulder. Care was taken also to ensure that the tip of the elbow was always firmly in contact with the support during efforts with triceps, as occasional subjects were noted to lift the elbow otherwise in an attempt to alter their leverage on the system. Despite all precautions, some activity would be expected in muscles fixating the shoulder joint, but this activity was not apparent from surface electromyography, nor did it become so when vibration was used.

Experiments were conducted in a quiet room, or with soft music playing in the background, according to the subjects' preferences. As far as possible the experimenters and the recording apparatus were kept out of the subjects' view. All subjects practised the tasks required, experienced muscle vibration, and were given an outline of the protocol to be followed, before the experiment was begun. In addition, a complete exercise trial involving muscle vibration, with all recording procedures working, was given when a subject was ready. This trial was disregarded for experimental purposes, although the subject did not know this: this trial served to allay any initial anxiety in the subject, and to allow all experimental procedures to be preceded by a previous period of exercise. The experiment commenced with a period of exercise 20 min after the trial, and successive periods followed with 20-min rest periods between. In the rest periods, subjects removed the mask or mouthpiece used for ventilatory measurements, and were encouraged to read.

Isometric exercise was performed for 2–8 min, usually 3 or 4 min. The exercise level chosen was between 20 and 50 % of the maximal voluntary contraction. To determine this maximum the subject was asked to make several maximal efforts of 2 or 3 sec duration: because of the instruction to avoid using the shoulders, most subjects probably registered tensions which were less than the true maximal tensions. Nevertheless, the level chosen was repeated in comparable manoeuvres of the experiment, and its absolute level in kilograms was known. Vibration of either the contracting muscle or its antagonist did not alter the maximum registered by a subject even if he was, for the purposes of this test only, allowed to move his shoulder and trunk as he chose. The subjects sat during the experiments facing the screen of an oscilloscope on which the tension achieved was displayed on one beam and the other beam was set at the desired level of tension: in exercise, they were asked to align the beams.

The sequence in which the steps of the experiment were conducted was chosen to minimize any complications arising from the effects of muscle fatigue (see Results section).

Recording. Arterial blood pressure, the electrocardiogram, ventilation, and end-tidal carbon dioxide were measured, and the tension achieved in the working arm was monitored.

Blood pressure was usually measured by sphygmomanometry in the nonexercising arm. For this, the bell of a stethoscope was strapped over the brachial artery, and a tube led from it over the subject's shoulder to an experimenter seated immediately behind. The blood pressure cuff was rapidly inflated by turning a tap from a drum charged to a pressure of about 200 mm Hg, and deflated in the usual way through a variable valve. Measurements were made one after another, the pressure in the cuff always dropping to zero between observations. Systolic and diastolic pressures were taken thus every 20–30 sec, the exact timing of the measurement being marked on the experimental record by the experimenter through a remote control marker. In a supplementary study, blood pressures were measured intra-arterially in three subjects with a transducer (SE Laboratories: SE 4–82) connected to a nylon cannula in the brachial artery. Ventilation was not measured in these three experiments. These studies were done with the informed consent of the subjects. The heart rate was counted from standard electrocardiograms.

The subjects breathed through a low resistance, small dead-space valve (Cunningham, Johnson & Lloyd, 1956) connected to a mouthpiece or to a tight-fitting, small dead-space face mask. They inspired room air. The expired gas was led through a curved metal tube immersed in ice, to remove moisture, and then through a gas-meter. Electrical contacts were arranged on the dial of this meter to produce a pulse on the record for every 5 l. of gas passing through it.

Expired gas was withdrawn at 30–60 ml./min and led through a CO_2 analyser. The output of this analyser gave end-tidal carbon dioxide tension.

The electrocardiogram, the ventilatory volume, the carbon dioxide tension, the tension recorded in the strain gauge, and the marker for the blood pressure observations, were all recorded with an ultra-violet-light recorder (SE Laboratories: SE 3006).

RESULTS

Repeated exercise and fatigue. Comparisons between responses to the same muscular effort repeated a number of times must allow for the possible influence of fatigue. Fatigue might alter the afferent neural activity from the working muscle which is responsible for cardiovascular and respiratory responses. Moreover, a fatigued muscle might require a greater central command to achieve a given tension than it would normally. Either effect would complicate the present study in which it is assumed that reflex activity is similar from trial to trial at a constant tension, and that the central command is altered only by the experimental manoeuvres with vibration.

To investigate the effects of fatigue, we asked subjects to make repeated efforts with only short recovery periods between them. When fatigued in this way, subjects showed greater than normal responses in blood pressure, heart rate, and ventilation to a given level of work. The pressor responses of a subject to the same work load repeated so frequently as to cause fatigue are shown in Fig. 4: both the heart rate and ventilation changed in a similar way, but these parameters did not return to control levels as quickly or precisely as blood pressure.

A full study of the effects of fatigue was not made here because of the difficulty in distinguishing between reflex and central influences. Nevertheless, the principal part of the present study was arranged so as to minimize any complications caused by fatigue. First, all studied contractions were less than half the maximum a subject could achieve, and were spaced 20 min apart to allow good recovery. Secondly, by using the first contraction period as a 'trial', it was possible to have each experimental contraction preceded by a contraction 20 min earlier. With such precautions, the reproducibility of responses to an effort simply repeated was good: the pressor response was most reliable (note its reproducibility before there was appreciable fatigue in the first three contractions shown in Fig. 4); the increments in heart rate and ventilation were also well reproduced, although slight shifts in the resting values did occur throughout the period of an experiment (e.g. see Fig. 5). As well as requiring only moderate efforts, and giving long periods for recovery, a further precaution was taken against interference from fatigue. Experiments were conducted in paired efforts of contractions with and without vibration: in these pairs the effort in which the central command was greater, according to the principle of our method, was done first. That is, a contraction with vibration was done first when vibration was intended to inhibit, and was done second when vibration was intended to assist. This way the effects of fatigue were working against the interpretation we came to put on our results, for central command was always greater in the first of a pair whereas fatigue could be greater only in the second of the pair.

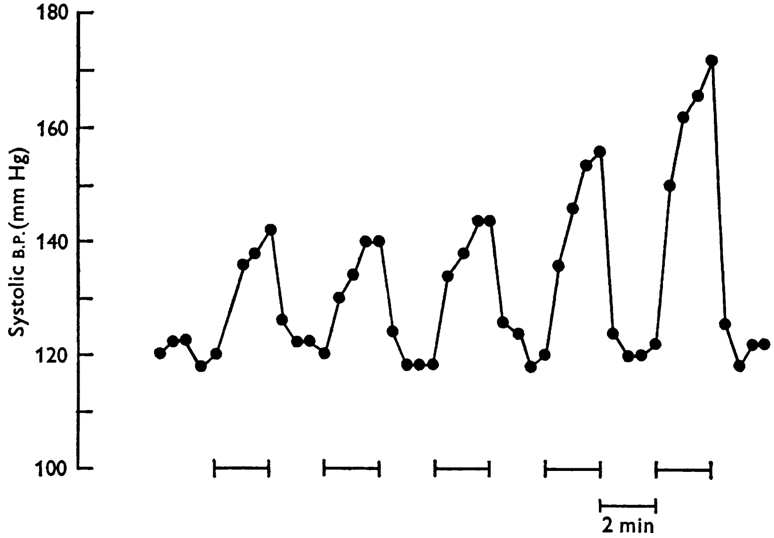

Fig. 4. Fatigue. The systolic blood pressure (B.P.) is shown during a period in which a subject made repeated isometric contractions of biceps to achieve a tension of 8 kg at the wrist, which was 40 % of his maximal voluntary contraction. Each contraction lasted 2 min, and there were recovery periods of 2 min between efforts. Each effort is shown by a bar underlying the plotted pressures. The pressor response to an effort was well reproduced for the first three efforts, then increased in the next two efforts. The subject was unable to maintain the same tension throughout a further 2-min effort.

Reduction of central command. Ideally, the experiment desired here was one in which a purely reflex contraction was compared with one of the same magnitude performed voluntarily. Such an experiment gave results in only one out of the ten satisfactory subjects, because most subjects produced reflex contractions of only 10–15 % of their maxima, levels which produce little or no cardiorespiratory responses when done voluntarily (Lind *et al.* 1966). In none of the subjects with these small reflexes was the vibration associated with increases in blood pressure, heart rate, or ventilation. One of our subjects, however, had a vibration reflex contraction of about 40 % of his maximum: his heart rate and ventilation increased in response to this contraction (blood pressure was not measured), and the same parameters increased more when he did a voluntary contraction of the same magnitude. These results strongly indicate a cardiorespiratory drive from central irradiation: nevertheless, it was a single experiment, and the subject was a physiologist who was familiar with the aims of our study.

In the later half of this study, the usual way of reducing the central command was to allow vibration to provide part of a given tension reflexly, while the subject contributed some voluntary command: this allowed study of tensions in the range which produce good cardiorespiratory responses. Reduction of the central command reduced the pressor, heart rate, and ventilatory responses seen at the same achieved muscle tension, as shown in Fig. 5. In this part of the study particularly, it was often found that one of the measured parameters was not clearly altered when others were: in this respect heart rate or ventilation was generally more difficult to separate clearly from the levels they attained in a simple voluntary contraction than was blood pressure, perhaps because of the slight variations observed even at rest in these parameters (e.g. heart rate in Fig. 5). Nevertheless, the manoeuvre used here to decrease the central command was never associated with increases in any of the measured parameters above the levels they attained during control efforts and clear cut decreases in one or more of the parameters were seen in eight out of ten experiments on five subjects.

A variation of the above method was used on three occasions to minimize the variability of heart rate responses. In this method a subject was asked to make a simple voluntary contraction during which vibration was applied for a time to give reflex assistance and then removed: this provided a period within a single contraction when the central command was reduced below the level at which it was held for the remainder of the contraction. During the period of vibration, the heart rate in each case fell below the level which it had attained during the simple voluntary contraction (see Fig. 6).

Increase of central command. As described in the Methods section, it was possible to require a greater than normal central command for given tensions by using vibration of an antagonist. When this was done blood pressure, heart rate, and ventilation increased more during a given effort when the central command was greater. This is shown in Fig. 7 for two levels of muscular tension achieved by a subject each at a normal and at an increased level of central command.

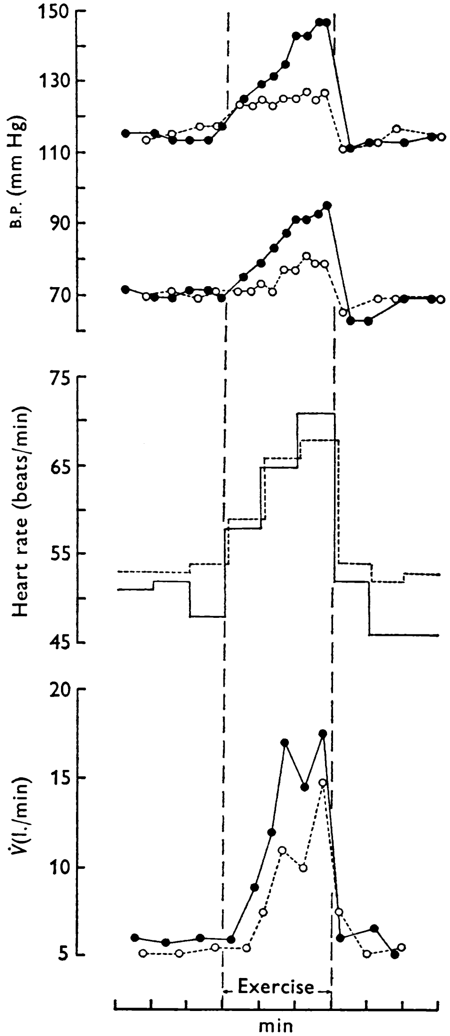

Fig. 5. Reduction of central command. Systolic and diastolic blood pressures (B.P.), heart rate, and ventilation ($\dot{V}$) are plotted before, during, and after two isometric contractions of biceps in which a tension of 3·2 kg was developed at the wrist (20 % of maximum). The responses to a normal contraction are shown by the filled circles and continuous lines; the responses when vibration was applied to allow a reduced central command are shown by the open circles and interrupted lines.

A similar experiment done in another subject is shown in Fig. 8. In this study the ventilatory response is shown together with end-tidal P_{CO_2} measurements. Again, the same tension achieved when the central command was greater was associated with increased ventilatory and heart rate responses. Results like those illustrated were obtained in all ten satisfactory subjects (in fifteen out of eighteen experiments.)

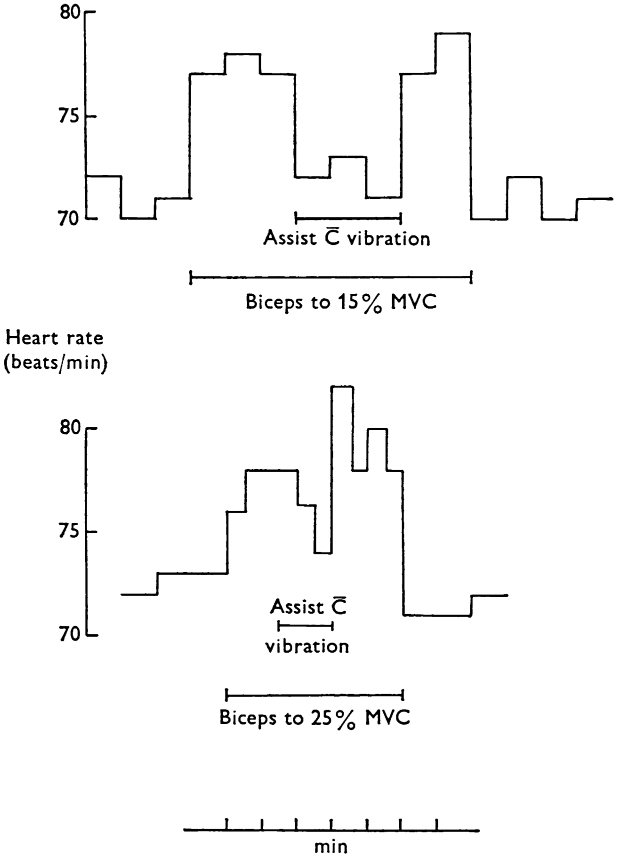

Fig. 6. Reduction of central command. Heart rate responses in two subjects during prolonged isometric contractions of biceps at 15 and 25% of the maximal voluntary contraction (MVC) tensions. In each subject vibration of the contracting biceps was used as described to reduce the central command during a period which commenced after contraction had begun and ended before the contraction had ceased.

Introspective analysis. Subjects were always asked, at the conclusion of an experimental series, to comment upon their experiences in the studies. All subjects found that each effort required of them was not difficult to begin with, but that it became more difficult as it continued. This is consistent with fatigue. All subjects found that vibration applied to either the contracting muscle or its antagonist required greater concentration in holding a desired tension. This was probably because of subtle proprioceptive illusions induced by the vibration (Goodwin, McCloskey & Matthews, 1972), which all subjects experienced. When vibration was applied to antagonistic muscles to require an increase of central command, all subjects felt that the effort required to achieve a given tension was greater. When vibration was applied to the contracting muscle itself to assist it

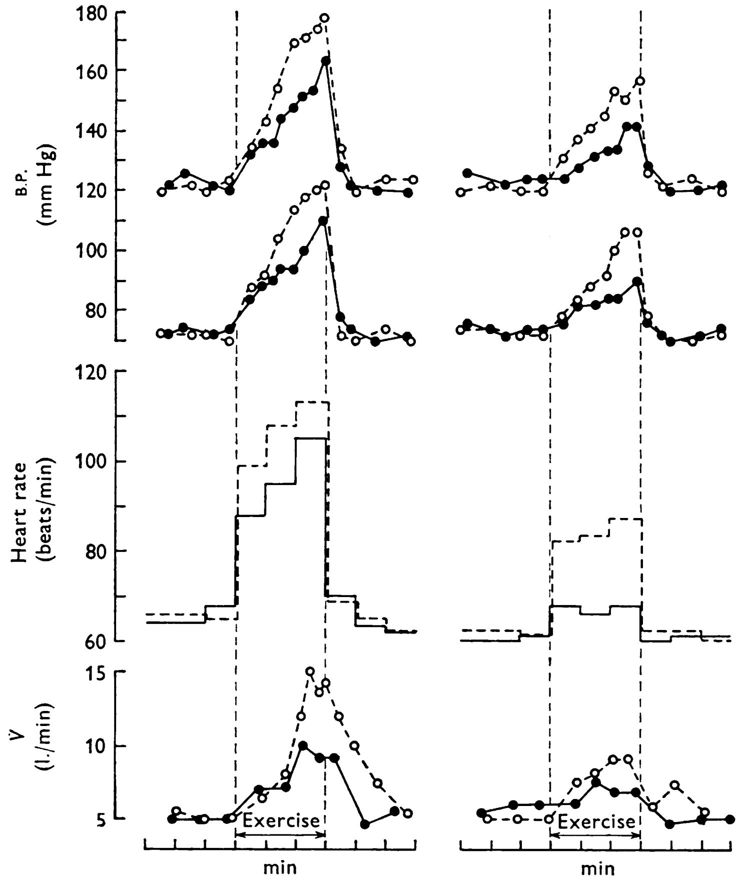

Fig. 7. Increase of central command. Systolic and diastolic blood pressures, heart rate, and ventilation are plotted before, during, and after two pairs of isometric contractions of triceps in which tensions of 4·9 kg (35 % of maximum) in the left panel, and 2·1 kg (15 % of maximum) in the right panel, were developed at the wrist. The responses when the central command to triceps was increased by vibration of biceps are shown by open circles and interrupted lines; and are to be compared with the responses to contractions of the same tension achieved normally, shown by filled circles and continuous lines.

reflexly so as to require less central command, a few subjects experienced that less effort was required; more often, subjects found the effort neither easier or harder (e.g. the subject in Fig. 4); and some subjects found the reflexly assisted effort more difficult (e.g. subjects of Fig. 5), perhaps because of the increased mental concentration required.

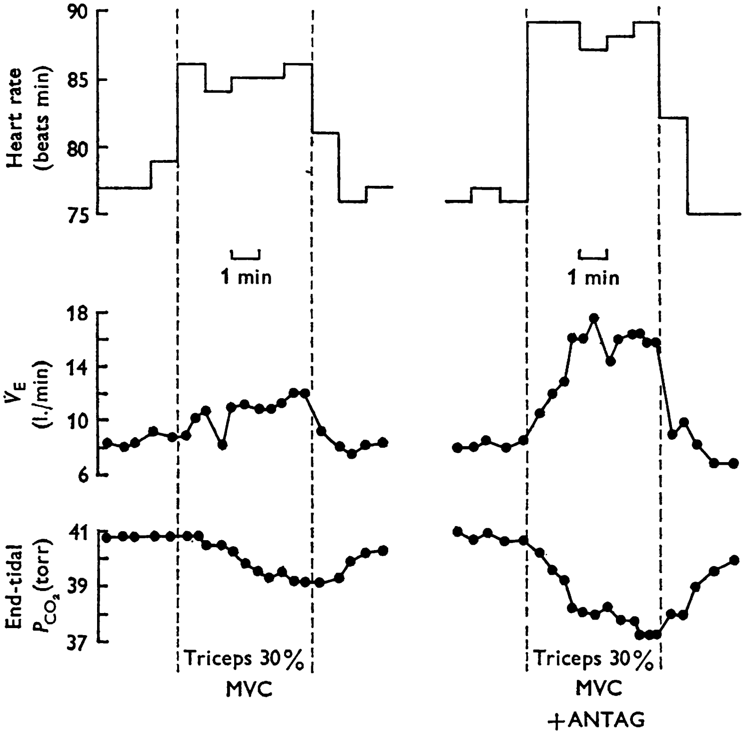

Fig. 8. Increase of central command. The heart rate, ventilation, and end-tidal CO_2 tension are plotted during two isometric contractions of triceps to achieve a tension of 5·5 kg (30 % of maximum) at the wrist. On the left are shown the responses to the contraction performed normally. On the right are the responses to a contraction of the same force in which the central command required was greater because of vibration applied to the antagonist, biceps.

DISCUSSION

The present experiments indicate that elements of the descending motor command stimulate increases in blood pressure, heart rate, and ventilation during voluntary muscular contraction. That such an effect might exist was suggested by Krogh & Lindhard (1913), who called it 'cortical irradiation'. Our experiments give no indication of the source of the irradiation, which might or might not be cortical.

The influence of command signals given to muscles unable to respond was investigated by Freyschuss (1970) who found that blood pressure and heart rate increased in subjects attempting to make handgrips with an arm paralysed with succinylcholine. Our own experiments of this type, done in subjects attempting handgrips in an arm paralysed by anoxia through vascular occlusion also showed increases in heart rate and blood pressure. Nevertheless, experiments of this type are unsatisfactory because subjects are aware of their inability to achieve the attempted task when acutely paralysed (Goodwin *et al.* 1972), and a considerable physiological stress may be involved.

Another method of looking for an effect of central 'irradiation' has been to reduce muscular strength without paralysis by partial curarization of human subjects. In this type of experiment a greater central command is required to achieve a given level of muscular work when the subject is weakened than normally, and the increases in ventilation, blood pressure, and heart rate accompanying the work are also greater (Ochwadt, Bücherl, Kreuzer & Loeschcke, 1959; Asmussen, Johansen, Jørgensen & Nielsen, 1965). These observations can also be taken to establish the importance of central irradiation, although Asmussen *et al.* preferred an alternative explanation. They argued that the work was achieved in the weakened state by an 'increased activation of the gamma loop', that this entailed a greater activity in the afferent nerves from muscle spindles, and that the enhanced cardiovascular and respiratory responses were consequent upon this increased peripheral afferent activity. This explanation of their results seems unlikely to be correct. Experiments on animals indicate that activation of muscle spindle primary afferents by vibration produces no appreciable ventilatory or cardiovascular responses (Hodgson & Matthews, 1968; D. I. McCloskey, P. B. C. Matthews & J. H. Mitchell, unpublished work), and nerve block of only the large myelinated afferents, which include afferents from muscle spindles and Golgi tendon organs, does not alter the cardiorespiratory responses mediated by muscle afferents during contraction (McCloskey & Mitchell, 1972). Moreover, the experiments reported here give no indication of a stimulus to the measured parameters by the excitation of muscle spindle primary afferents by vibration. For these reasons, the experiments with partial curarization also argue for the importance of central irradiation.

The present experiments have used a different approach to answer the same question. Vibration is known to be a powerful stimulus to the primary endings of muscle spindles in animals (Brown, Engberg & Matthews, 1967; Matthews, 1972) and is assumed to act through these same afferents to cause the tonic vibration reflex in man (De Gail *et al.* 1966; Hagbarth & Eklund, 1966). It was used here to assist or to inhibit reflexly a voluntary isometric contraction. That such assistance or inhibition did occur is shown by the effects of suddenly removing the vibration while a subject maintained a constant effort, as was shown in all experiments, and illustrated in Fig. 3. Indeed, this demonstration indicates that the central command was altered according to the design of the experiment whether or not the assumption is correct that the mechanism involved activation of muscle spindle primary afferents.

The method also depends on the assumption that the activity of muscle afferents involved in cardiorespiratory reflexes remains similar in compared trials. Clearly the activity of primary afferents from the muscle spindles differed, as also probably did activity of afferents from spindle secondary endings, but, as discussed above, there is little reason to implicate these afferents in cardiorespiratory reflexes. It is known that several important muscle metabolites (lactate, ATP, creatine phosphate, glycogen) come to attain very similar levels during each of a series of contractions except the first (J. Karlsson, personal communication). The first contraction was commonly rejected for experimental purposes in our studies, so that it is likely that the muscle was in comparable biochemical state in compared trials. It has been explained above (Results, section 1) how precautions were taken against complications that might have been caused by fatigue.

The present experiments might be influenced by the contraction of muscle groups other than those primarily involved in the study. For example, muscles stabilizing the shoulder joint might vary their activity from trial to trial, although we were not able to detect such changes electromyographically. However, Lind *et al.* (1966) found that the cardiovascular responses to an isometric effort varied according to the proportion of its maximum which a muscle group was achieving, and that if two muscle groups were contracting the responses were determined by the group achieving the greater proportion of its own maximum. Thus, variations in the activity of accessory or other muscles in our study would be expected to influence the responses only if they were achieving a greater proportion of their own maxima than the experimental muscle was of its maximum. That activity of such magnitude could have occurred without being detected is most unlikely. Activity in the vibrated antagonist of a contracting muscle could have presented a more specific problem, because this would have meant that the voluntarily contracted muscle would have had to increase its own tension by an amount equal to that elicited by vibration in the antagonist in order to register the required tension externally. This possibility was excluded in all cases where it might have occurred by palpation, which could readily detect contractions of 2 % of maximum, and on occasion by less sensitive electromyographic testing.

All our subjects thought any effort was more difficult when an antagonist was vibrated, and it might be argued that their responses were to the subjective assessment of difficulty rather than to the magnitude of the descending command signal. This objection also applies to the partial curarization experiments of Ochwadt *et al.* (1959) and Asmussen *et al.* (1965). Nevertheless, it carries less weight when it is noted that subjects in whom vibration supplied reflex assistance did not usually report that the effort, although it produced smaller cardiorespiratory responses, was subjectively easier: some even noted that such assisted efforts were subjectively more difficult. These observations suggest that emotional factors did not play a significant part in the present study.

Once it is accepted that the neural drive to the mass transport systems in exercise has both central command and peripheral reflex components, the relative contributions made by both become of interest. This introduces several problems, First, it cannot be concluded that the contribution of each component drive to each cardiovascular and respiratory parameter is identical. Nor can it be assumed that the component drives simply add to produce their combined effect. For example, Asmussen, Nielsen & Wieth-Pedersen (1943) concluded that central irradiation gave no responses because the responses caused by electrical stimulation of muscle through the skin gave similar responses to similar contractions voluntarily achieved: such a conclusion is based on the assumption that peripheral and central mechanisms are additive. Even if these experiments, done on only two subjects, could be repeated, they would not mean that central radiation was without effect, for simple neural occlusion is possible, Moreover, it should be noted that the parameters measured here, and others which may be found to be similarly influenced by both central irradiation and reflex mechanisms, may interact one with another through other mechanisms (e.g. a pressor response tends to slow the heart rate through baroreceptor reflexes), so that the change seen in any single parameter will be induced by the two parts of the neural drive acting together with influences brought into play indirectly by other responses.

The present experiments seemed to allow the interesting possibility that the reflex component and the central component of the cardiorespiratory drive in isometric exercise could be varied more or less independently. Thus, it might have been possible to work out how the two components interacted quantitatively. This would have been feasible if a satisfactory means could have been devised for estimating the magnitude of the command during assisting or opposing vibration. The steady tension reached after the sudden removal of the vibrator might have served as such a measure of the prevailing central command. However, in practice the tension changes seen in these circumstances, examples of which are illustrated in Fig. 3, were too variable in size and too short in duration to give much confidence in this method. Consequently, the present results constitute qualitative evidence for the existence of a central component, without showing how this should be expected to summate with the better known reflex contribution from the periphery.

We thank Dr P. Sleight for his assitance with intra-arterial recording, and Pifco Ltd. for the gift of vibrators used in this study.

REFERENCES

ASMUSSEN, E., JOHANSEN, S. H., JØRGENSEN, M. & NIELSEN, M. (1965). On the nervous factors controlling respiration and circulation during exercise; experiments with curarization. *Acta physiol. scand.* **63**, 343–350.

ASMUSSEN, E., NIELSEN, M. & WIETH-PEDERSEN, B. (1943). Cortical or reflex control of respiration during muscular work? *Acta physiol. scand.* **6**, 168–175.

BROWN, M. C., ENGBERG, I. & MATTHEWS, P. B. C. (1967). The relative sensitivity to vibration of muscle receptors in the cat. *J. Physiol.* **192**, 773–800.

COOTE, J. H., HILTON, S. M. & PEREZ-GONZALEZ, J. F. (1971). The reflex nature of the pressor response to muscular exercise. *J. Physiol.* **215**, 789–804.

CUNNINGHAM, D. J. C., JOHNSON, W. G. H. & LLOYD, B. B. (1956). A modified 'Cormack' respiratory valve. *J. Physiol.* **133**, 32–33*P*.

DE GAIL, P., LANCE, J. W. & NEILSON, P. D. (1966). Differential effects on tonic and phasic reflex mechanisms produced by vibration of muscles in man. *J. Neurol. Neurosurg. Psychiat.* **29**, 1–11.

FREYSCHUSS, U. (1970). Cardiovascular adjustment to somatomotor activation. *Acta physiol. scand.* suppl. 342, 1–63.

GOODWIN, G. M., MCCLOSKEY, D. I. & MATTHEWS, P. B. C. (1972). The contribution of muscle afferents to kinesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. *Brain* (in the Press).

GOODWIN, G. M., MCCLOSKEY, D. I. & MITCHELL, J. H. (1971). Cardiovascular and respiratory responses to changes in central command during isometric exercise at constant muscle tension. *J. Physiol.* **219**, 40–41*P*.

HAGBARTH, K.-E. & EKLUND, G. (1966). Motor effects of vibratory muscle stimuli in man. In *Muscular Afferents and Motor Control*, ed. by GRANIT, R., pp. 177–186. Stockholm: Almqvist and Wiksell.

HODGSON, H. J. F. & MATTHEWS, P. B. C. (1968). The ineffectiveness of excitation of the primary endings of the muscle spindle by vibration as a respiratory stimulant in the decerebrate cat. *J. Physiol.* **194**, 555–563.

KAO, F. F. & RAY, L. H. (1954). Respiratory and circulatory responses of anesthetized dogs to induced muscular work. *Am. J. Physiol.* **179**, 249–254.

KROGH, A. & LINDHARD, J. (1913). The regulation of respiration and circulation during the initial stages of muscular work. *J. Physiol.* **47**, 112–136.

LIND, A. R., MCNICOL, G. W. & DONALD, K. W. (1966). Circulatory adjustments to sustained (static) muscular activity. In *Proceedings of the International Symposium on Physical Activity in Health and Disease*, ed. by EVANG, K. & ANDERSEN, K. L., pp. 36–63. Norway: Universitetsforlaget.

MCCLOSKEY, D. I. & MITCHELL, J. H. (1972). Reflex cardiovascular and respiratory responses originating in exercising muscle. *J. Physiol.* (in the Press).

MATTHEWS, P. B. C. (1972). *Muscle Receptors and Their Central Actions.* London: Arnolds.

Myhre, K. & Andersen, K. L. (1971). Respiratory responses to static muscular work. *Resp. Physiol.* **12**, 77–89.

Ochwadt, B., Bücherl, E., Kreuzer, H. & Loeschcke, H. H. (1959). Beeinflussung der Atemsteigerung bei Muskelarbeit durch partiellen neuromuskulären Block (Tubocurarin). *Pflügers Arch. ges. Physiol.* **269**, 613–621.

Wiley, R. L. & Lind, A. R. (1971). Respiratory responses to sustained static muscular contractions in humans. *Clin. Sci.* **40**, 221–234.