Modulation of postural reflexes by voluntary movement¹

2. Modulation at an inactive joint

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SUMMARY We have observed that there is a brief, 400 msec period of widespread facilitation of both the Hoffmann and the tendon-jerk reflexes associated with the initiation of a variety of local, voluntary, isometric efforts. It is suggested that the site of this facilitation lies within the spinal cord. We have also observed that this period is followed, for the Hoffmann reflex, by a period of spinal inhibition. By contrast, the tendon-jerk is facilitated, at a reduced level, for at least another 500 msec by mechanisms probably working at the muscle spindle. These results are discussed in comparison with experiments involving activation of the reflex agonist and antagonist muscles. It is proposed that voluntary control of the locomotor system is organized through separate mechanisms for muscle recruitment and for regulation of the sensitivity of the myotatic reflex loop.

The performance of a voluntary movement may be considered as two coordinated but distinguishable tasks. The obvious task is the execution of the intended movement—stepping with one's foot, for example. Inseparable from this act are the associated postural compensations which are made throughout the entire musculoskeletal system.

Compensation is required because of three physical forces that may be generated by a movement. Newton's third law of motion tells us that to every action there is an equal and opposite reaction. Thus, motion of a limb tends to push the body in the opposite direction. The second disturbing force arises from the displacement of the body's centre of gravity. The third is produced by interaction with other physical objects and forces.

We are not normally aware of making these compensations for our every move, nor even of the need for them. It is only occasionally, as when ice skating or falling for example, that we notice the existence of these compensating actions by their ineffectuality under those

peculiar conditions. Our reason for not normally noticing lies, in part, in the automaticity of the compensations. Of equal importance, though, is that they may occur in two ways: one patent, the other latent.

The obvious compensation to a mechanical disturbance is to tense up the muscles which will counteract it. Thus, in many common motor tasks, from lifting a weight to catching a thrown object, we brace our arms and set our feet automatically. This not only creates forces in opposition to the disturbance but increases the mechanical impedance of the muscles themselves (Agarwal, Berman, and Stark, 1970). This type of response we can term 'active compensation', since suitable mechanical events, force and movement, are generated by neural commands from the central nervous system. There is thus an overt recruitment of appropriate muscles in anticipation of the forthcoming disturbance (Belen'kii, Gurfinkel, and Pal'tsev, 1967).

The second type of compensation is not readily manifest. This we shall call 'adaptive compensation' and it is effected by alteration of the sensitivity of postural reflex mechanisms so that disturbances may be dealt with rapidly at

¹ This work was supported in part by NSF grant GK-17581 and a PSL research grant.

lower levels of the neural hierarchy. Such a mechanism reveals its existence only in the presence of an actual disturbance to which the reflex has been conditioned.

The experiments presented here were designed to reveal the time course of this adaptive compensation to a variety of voluntary efforts. The site of adaptation, within the anterior horn of the spinal cord or at the muscle spindle, is also considered.

The well-known influence of voluntary muscle contraction upon the monosynaptic reflexes (studied as the Jendrassik manoeuvre (Jendrassik, 1883)) has been subject to fluctuating opinion. The tendon-jerk reflex is long known to be facilitated, presumably by fusimotor activation of the muscle spindles (Paillard, 1955) but early investigators (Sommer, 1940; Paillard, 1955; Buller and Dornhorst, 1957) disagreed on the existence of facilitation of the Hoffmann reflex (H-reflex) (Hoffmann, 1922; Magladery and McDougal, 1950). More recently, it has been demonstrated that not only is facilitation of the H-reflex present (Landau and Clare, 1964), but that it survives procaine block of the peripheral nerve which abolishes the tendon-jerk (Clare and Landau, 1964). These authors concluded that intraspinal, rather than fusimotor, mechanisms produced the Jendrassik phenomenon. Most recently, a synthesis of these dialectical viewpoints has appeared (Gassel and Diamantopoulos, 1964a, b; Clarke, 1967) which proposes a central influence facilitating the H-reflex and the tendon-jerk but suggests additional fusimotor excitation which increases and prolongs the duration of tendon-jerk facilitation. Our findings concur with these latter conclusions.

METHODS

In the series of experiments reported here, a subject made a sequence of highly repeatable, voluntary, isometric efforts (usually 70 to 100). At different moments before, during, and after these efforts, a reflex stimulus was delivered to the relaxed left leg, which was not involved in the voluntary effort. These stimuli were either taps to the achilles tendon to elicit the tendon-jerk reflex or electrical shocks to the tibial nerve in the popliteal fossa to elicit the H-reflex (Hoffmann, 1922; Magladery and McDougal, 1950; Gottlieb and Agarwal, 1973). Measurements of the peak-to-peak amplitude of the

synchronized reflex electromyogram (EMG) burst in the soleus muscle were used to determine the relative sensitivity of the reflex arc.

Our subjects (three male, one female) were seated comfortably in a chair. The relaxed left leg, in which the reflex was elicited, was strapped to a rigid wooden foot rest. Four types of voluntary, isometric efforts were made. These were (1) a vigorous plantarflexion of the right foot, (2) a vigorous dorsiflexion of the right foot, (3) a vigorous pull by the two arms, in opposition to each other (the classical Jendrassik manoeuvre), and (4) an inverse Jendrassik manoeuvre in which the opposed, contracted arm muscles were suddenly relaxed. For the first two types of efforts the right foot was strapped to a rigid aluminium foot plate which had strain gauges for measuring the voluntary foot torque. This apparatus is described in the preceding paper (Gottlieb and Agarwal, 1973). For the arm efforts, both hands grasped a special U-shaped aluminium strip which also had strain gauges for force measurements.

The H-reflex was elicited by a Grass S-8 stimulator connected through an SIU5 isolation unit. Cutaneous stimulating electrodes were strapped posteriorly in the popliteal fossa and anteriorly above the knee.

FIG. 1. *Experimental apparatus for eliciting the achilles tendon-jerk reflex (left foot) and measuring voluntary foot torque (right foot). The hammer is a modified 12 in. high fidelity speaker.*

The tendon-jerk was elicited by a specially designed electro-mechanical hammer drawn in Fig. 1. The hammer is basically an Acoustic-Research 12 in. speaker. Portions of the cone were cut out to diminish air resistance. To the centre of the cone was glued an 18.7 cm (8.5 in.) long plexiglass shaft. At the top of this shaft, an aluminium 'hammer head' with strain gauges for force measurement was mounted. The tip of this head was coated with a silicon rubber adhesive to cushion the blow on the tendon. This hammer was driven by an Inland 100 W dc power amplifier. At maximum output a 12 kg blow 5 msec wide (at one half the peak amplitude) could be delivered (1.65 cm (0.75 in.) travel) to the tendon, a blow more than adequate to elicit a maximal stretch reflex (Agarwal, Berman, Löhnberg, and Stark, 1970; Dietrichson, 1971).

The reflex electromyograms were recorded with 1 cm diameter disc electrodes, taped about 3 cm apart over the soleus muscle. All electrodes were coated with Sanborn Redux Creme.

The subjects were asked to make their efforts in a highly repeatable manner. To aid them, they were provided with both an audio (a tone burst) and a visual (movement of an oscilloscope trace) warning to commence the voluntary manoeuvre. The visual warning was the start of a slow (one second duration) trace of the beam across the face of a Tektronix RM564 memory oscilloscope. This trace was deflected vertically by the force of the voluntary effort. One such display is shown in Fig. 2. The subject could thereby see precisely how his efforts were

FIG. 2. Typical memory oscilloscope display observed by the subject during an experiment (72 traces superimposed). Upper traces: voluntary force (increasing downward). Lower traces: H-reflex EMG, 2.0 mV/unit. Time scale 0.1 sec/unit.

going. The interval between the audiovisual warning and the start of the movement was typically 168 msec with a standard deviation of 24 msec (subject GCA).

The time interval between the audiovisual warning and the reflex stimulus (interstimulus interval) was controlled by an IBM 1800 digital computer which recorded the voluntary force and the reflex EMG. Usually, six stimuli were delivered at each of 12 different interstimulus intervals ordered in a random sequence.

For each group of six stimuli delivered at one of these interstimulus intervals, the actual time interval between the delivery of the reflex stimulus and the initiation of the voluntary effort (Gottlieb and Agarwal, 1973) was measured and the average value plotted as the abscissa for the data that will be presented.

In all experiments, the base level of reflex activity was defined as the average amplitude of six reflex responses, elicited 50 msec before the audiovisual signal was presented. Thus, we had an alert and prepared subject but one who had not yet begun the execution of the voluntary effort. The time interval between successive reflex stimuli, 7 to 10 seconds was too long to allow successful anticipation of the signal.

The subjects were instructed to maintain their efforts until after the reflex eliciting stimulus had been delivered. No change in voluntary activity was initiated after the reflex stimulus was delivered could affect the monosynaptic reflex response to the stimulus.

For the inverse Jendrassik manoeuvre, the subject was given a signal to contract his arms six to eight seconds before the stimulus. It has been shown that the effects of such a contraction are transient (Buller and Dornhorst, 1957; Clarke, 1962). Therefore, in spite of the sustained contractions, by the time the signal to relax was given the subject could be assumed to have returned to the baseline of reflex excitability defined in the same manner for these experiments as for the others. The inverse Jendrassik manoeuvre was thus a phasic event following a sustained voluntary effort.

In a single experimental session, either the H-reflex or the tendon-jerk reflex was used as the test and two or three runs would be made, each with a different type of voluntary effort. In all cases the EMG in the stimulated left leg was monitored to verify that the muscles were not contracted other than by the reflex.

RESULTS

Two series of experiments using the H-reflex are shown in Figs 3 and 4. These show the normalized

FIG. 3. *Relative H-reflex modulation during a voluntary movement. ▲ plantarflexion, + dorsiflexion, ○ Jendrassik manoeuvre. Subject GCA. In this and the remaining figures, each point is the average of six responses. Solid lines are sixth order regression curves. The computer has plotted straight line segments, connecting values of the regression curve at abscissa values of the data points.*

FIG. 4. *Like Fig. 3. Plantarflexion and Jendrassik manoeuvre. Subject SFH. Dorsiflexion subject GLG.*

average amplitude of the reflex EMG (ordinate) plotted against the time interval between the recording of the reflex EMG and the start of the voluntary effort. The ▲ points were recorded during a plantarflexion of the right foot, + points during a dorsiflexion of the right foot, and ○ points during a Jendrassik manoeuvre.

We may observe several characteristics in these curves. The initial effect of all three voluntary efforts is a facilitation of the H-reflex which

precedes the start of a measurable effort by about 100 msec, reaches its maximum about 50 msec after the effort begins, and is followed by a period of inhibition (in all but one part of Fig. 4) which lags the initiation by about 250 msec.

In Figs 5 and 6, a similar series of experiments is illustrated. In these, however, the reflex elicited is an achilles tendon-jerk. Again, the symbols ▲, +, and ○ indicate plantarflexion and dorsiflexion of the right foot and Jendrassik manoeuvres respectively.

As in the H-reflex experiments, all voluntary efforts cause an initial facilitation which precedes them by about 100 msec. In contrast to H-reflex experiments, the duration of tendon-jerk

FIG. 5. *Relative tendon-jerk modulation during a voluntary movement. ▲ plantarflexion, + dorsiflexion, ○ Jendrassik manoeuvre. Subject GCA.*

FIG. 6. *Like Fig. 5. Subject GLG.*

facilitation is 750 msec or more and in the time interval investigated, no inhibitory phase was observed. We may also note that in the experiments illustrated, the maximum facilitation of the tendon-jerk is usually greater than that of the H-reflex.

Finally, in Figs 7 and 8 we show the time course of the influence of Jendrassik and inverse Jendrassik manoeuvres on the H-reflex (Fig. 7) and the tendon-jerk reflex (Fig. 8). The $\odot$ points were recorded during a Jendrassik manoeuvre and the $\times$ points were recorded during the inverse Jendrassik manoeuvre.

(Note, in all Figures, that the vertical scales have been chosen to emphasize the observed variations of the data.)

FIG. 7. Relative H-reflex modulation during a Jendrassik manoeuvre ($\odot$ points) and an inverse Jendrassik manoeuvre ($\times$ points). Subject GCA.

FIG. 8. Relative tendon-jerk modulation during a Jendrassik manoeuvre ($\odot$ points) and an inverse Jendrassik manoeuvre ($\times$ points). Subject GLG.

DISCUSSION

The uniform effect of all voluntary efforts that we have studied using both electrical and mechanical stimuli is an early facilitation of the monosynaptic reflex which lasts at least through the dynamic phase of the effort. In the case of the H-reflex, this facilitation must almost certainly be mediated by regulation of the central excitability or gain—the adjustment of the sensitivity of the reflex loop (Clare and Landau, 1964; Landau and Clare, 1964; Gottlieb and Agarwal, 1973).

It has been our observation (see also Gassel and Diamantopoulos, 1964a), that the facilitation of the stretch reflex is more pronounced than that of the H-reflex. We are not certain of this, since considerable care must be taken (which we did not take) to assure that equivalent stimulus strengths are used in order to allow facilitating influences to act upon equivalent subliminal fringes. Greater tendon-jerk facilitation is not unexpected, since it is subject to two modulating inputs while the H-reflex admits only one. (Although Ia afferent activity can be expected to have some influence on the amplitude of an H-reflex response, we can find no support for a suggestion that significant reflex facilitation can be generated over this pathway unaccompanied by an observable activation of the alpha motoneurone pools).

It is interesting to observe in Figs 7 and 8 that an inverse Jendrassik manoeuvre also produces the early facilitation of both the tendon-jerk and the H-reflex. However, the late phase of tendon-jerk facilitation produced by voluntary muscle contractions is considerably reduced or absent. If no further changes in voluntary effort are made, facilitation of the tendon-jerk disappears within 10 seconds (Clarke, 1967) and of the H-reflex within one to two seconds (Dietrichson, 1971).

The brevity of the interval of H-reflex facilitation and the subsequent inhibition probably account for the diverse reports in the literature.

The influences of sensory stimuli on the excitability of the monosynaptic reflex arc have been recognized for almost as long as have been motor influences (Bowditch and Warren, 1890). Subsequent to the experiments described above, further tests were made using the same audio-

visual and reflex eliciting stimuli but with the subject instructed merely to sit and observe and to make no voluntary response. No variations in reflex amplitude with intervals between stimuli were observed.

This apparent contradiction with previous work (Bowditch and Warren, 1890; Paillard, 1955; Coquery, 1969) can probably be ascribed to the fact that our sensory stimuli were of a very gentle nature intended to alert but not disturb either subjects or experimenters. The tone (1 kHz ring, decaying over one to two seconds) was in fact similar in nature to those which inform you that you have just missed the lift. By contrast, Bowditch and Warren (1890) produced auditory stimuli by 'dropping a large paper torpedo near the head of the individual experimented on'. More recent investigators have also used intense, if more sophisticated, sensory stimuli.

Since the same audiovisual stimulus was used in all our experiments, the difference in the evolution of H and tendon-jerk reflexes cannot in any case be so explained. It is far more reasonable to attribute the prolonged facilitation of the tendon-jerk, in the face of H-reflex inhibition which is presumably in the same synaptic pathway, as reflecting fusimotor excitation of the muscle spindle (Paillard, 1955).

We must also note that our data on the inverse Jendrassik manoeuvre may not be in agreement with those of Paillard (1955, p. 208, Figs 49, 50) who observed only inhibition of both H and tendon-jerk reflexes after such a manoeuvre. Whether this is ascribable to difference of experimental techniques (he used repetitive reflex stimuli at 1–1.5 sec intervals) has not been determined.

CONCLUDING REMARKS

The tensing of remote muscles before the initiation of a voluntary movement, or active compensation, has been long recognized as part of the organizing pattern of motor control. We are proposing that the phenomena displayed by the Jendrassik manoeuvre, the general transient facilitation of the monosynaptic stretch reflex which we term adaptive compensation, play a very similar role. Both tend to fix the skeleton and thereby provide a rigid platform from which voluntary movements may be launched.

We can further note that the similarity of Jendrassik and inverse Jendrassik effects on the monosynaptic reflexes suggests that the 'adequate stimulus' is not necessarily muscle contraction but change in muscle activity. As there is at least one report contradicting these results (Paillard, 1955), however, such a conclusion must be very tentative.

Under physiological conditions, such modulation of reflex sensitivity does not necessarily lead to motor unit recruitment unless there is actual muscle stretch. For this reason we call this adaptive rather than active compensation. The virtues of such adaptive compensation are two fold. On one hand, there is an economy of effort. Muscles are recruited only with cause and in proportion to actual need. On the other hand, the computations required of the central nervous system to control the peripheral motor system are simplified, since less prediction of the course of the voluntary movement is required. The motor system merely takes advantage of the natural self-correcting properties of a negative feedback system by raising the closed-loop gain.

We may also note a considerable similarity between the time course of the early phase of facilitation shown here, and the facilitation of the monosynaptic reflex observed in the active limb during a voluntary effort (Kots, 1969; Gottlieb, Agarwal, and Stark, 1970; Coquery and Coulmance, 1971; Gottlieb and Agarwal, 1973). This facilitation appears about 100 msec before the initiation of the movement,¹ reaches its maximum within about 50 msec after the start, and has a total duration of about 400 msec.

We believe that these are related phenomena which are manifestations of a rather general principal of voluntary motor organization. There is a general stiffening of the musculo-skeletal system for stability, a quickening of the dynamic properties of the agonist reflex arc by increasing reflex sensitivity, followed by muscle activation and finally inhibition of antagonistic reflex arcs. Voluntary control of the motor system may be recognized as the conscious generation of muscle forces and joint rotations accompanied by an on-going regulation of

¹ The work of Kots (1969) indicates that reflex facilitation begins about 60 msec before the start of the EMG in the active muscle. There is about a 50 msec interval from the appearance of the EMG to the start of measurable force we so define as the initiation of the movement.

motor system dynamics to *adapt* and *tune* the peripheral portions of the motor system to its changing environment.

We wish to thank Dr. P. B. C. Matthews for his advice and criticism of the manuscript, Ms. Virginia Samter for her drawing of Fig. 1, and Ms. Ada Rahn for assistance in performing the experiments.

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