

## SUBJECT INSTRUCTION AND LONG LATENCY REFLEX RESPONSES TO MUSCLE STRETCH

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### SUMMARY

1. Surface electromyographic recordings were made in eight normal subjects from the isometrically contracting elbow flexors before and during forcible extension of the elbow through 7° in 50–150 msec.

2. When the subjects were instructed prior (2–5 sec) to a forthcoming stretch to 'resist' or to 'let go', they could reliably enhance or suppress e.m.g. activity occurring between 40 and 70 msec from commencement of the stretch. Such e.m.g. activity represents a 'long-latency' (or 'M2') reflex response: it occurs with a latency longer than the spinal segmental monosynaptic reflex, but shorter than a voluntary reaction time. When the subjects were given their instructions (by means of a light) at the moment the stretch commenced, however, none of them could adjust the long-latency reflex appropriately.

3. It is concluded that central, evaluative processes commencing at the time of a perturbation cannot influence long-latency reflex responses to that perturbation.

### INTRODUCTION

It is now well established that the electromyographic response to the sudden stretch of a voluntarily contracting muscle in a human subject usually has two reflex components: an early one which occurs at a latency consistent with its following the segmental, monosynaptic pathway of the tendon jerk and a later, commonly larger, one occurring at a longer latency (Hammond, 1956, 1960; Tatton, Forner, Gerstein, Chambers & Liu, 1975; Evarts & Granit, 1976; Evarts & Vaughn, 1978; Melvill Jones & Watt, 1971; Allum, 1975; Marsden, Merton & Morton, 1976, 1977; Iles, 1977). These responses, which have been termed M1 and M2 responses (cf. Tatton *et al.* 1975), occur at latencies shorter than a voluntary reaction time. In the isotonically contracting long flexor of the thumb (Marsden *et al.* 1976) or the expiratory intercostal muscles (Newsom Davis & Sears, 1970), the M1 response is usually absent but the M2 response is prominent. The M1 response is more dependent than the M2 on the velocity of stretching so that at slower velocities of stretch the M1 response may not be evoked while the M2 remains little affected (Evarts & Vaughn, 1978). Iles (1977) has recently offered good evidence that the M2 response, like the

M1, is evoked through intramuscular receptors. Recent interest in long-latency responses to muscle stretch has centred on the proposal by Phillips (1969) that such responses may follow a supraspinal, specifically a transcortical, reflex pathway (e.g. see Phillips & Porter, 1977; Evarts & Granit, 1976).

Hammond (1956, 1960) first drew attention to the ability of normal subjects to enhance or suppress the longer latency response (M2) according to their preformed intention to 'resist' or to 'let go' upon presentation of an unexpected stretch. This ability has now been demonstrated in several different human muscles, and in different experimental situations (Evarts & Granit, 1976; Evarts & Vaughn, 1978; Iles, 1977; Newsom Davis & Sears, 1970). It is of interest, however, that in an extensive study of long-latency responses in the isotonically contracting long flexor of the thumb Marsden *et al.* (1976) have been unable to demonstrate this ability.

In 1970 Newsom Davis & Sears presented another view of the long-latency response. These workers had shown that the long latency (50–60 msec) 'excitatory response' recorded in expiratory intercostal muscles which were suddenly loaded could be enhanced or reduced, like the long-latency responses described by Hammond and others, according to the instruction given to the subject prior to the loading. They saw as an essential feature of the response that it was preceded by a *delay*, and they discussed the possible reflex basis for this delay. The delay, they argued, 'allows time for the significance of the unpredicted input to be evaluated centrally so that the subsequent reflex control by the spindle loop is, under the new mechanical conditions, appropriate to intent'. This hypothesis was subsequently amplified and discussed by Sears (1971, 1973, 1974) and has been suggested as an explanation for other findings (e.g. Gottlieb & Agarwal, 1978). Whereas other workers had regarded the voluntary control of the M2 response simply as an example of *pre-setting*, the hypothesis of Newsom Davis & Sears (1970) gave it further significance. They envisaged a process of neural 'evaluation' going on in the time between presentation of a load and the reflex response to it. The long latency of the reflex was therefore seen as a delay permitting central evaluation of the load and resulting in a reflex response which was appropriate to intent (that is, matched to the succeeding voluntary response). Later it was stressed that the duration of this delay matched 'the duration of the minimal processing period for the generation of a percept following peripheral nerve stimulation' (Sears, 1973; see also, Sears, 1974).

This hypothesis could be taken to suggest that long-latency reflex action could be modified, in a period shorter than a voluntary reaction time, according to a process of evaluation which commences on presentation of the load. If correct, this possibility would significantly blur the distinctions presently recognized between 'voluntary' and 'reflex' actions. The studies we report here were designed to test this possibility.

#### METHODS

In order to see whether long-latency reflex responses to muscle stretch could be modified by central, 'evaluative', processes commencing at the time of the stretch, we compared the abilities of subjects to modify these responses in two experimental conditions. In the first part of the experiment subjects received a series of forty forcible extensions of the elbow in which each extension was *preceded* (2–5 sec) by an oral instruction to 'resist' or to 'let go' in response to it. These instructions were given in random order. In the second part of the experiment subjects

again received a series of forty forcible extensions of the elbow, but now with the instruction to 'resist' or to 'let go' given *at the moment the extension commenced*. These latter instructions usually took the form of a bright line, which appeared on the oscilloscope screen immediately in front of the subject when he was to 'resist' the pull, and which failed to appear when he was to 'let go'. In two subjects the 'simultaneous' instruction to 'resist' was given as a brief tap ( $\sim 2$  msec) on the wrist immediately prior to commencement of a pull instead of as a bright line. Instructions given at commencement of a pull were also given in random order. Subjects were given a brief training period (5–10 min) in which to acquaint themselves with the tasks required. Brief rest periods (1–2 min) were permitted when the subjects requested them and between the two parts of the experiment.

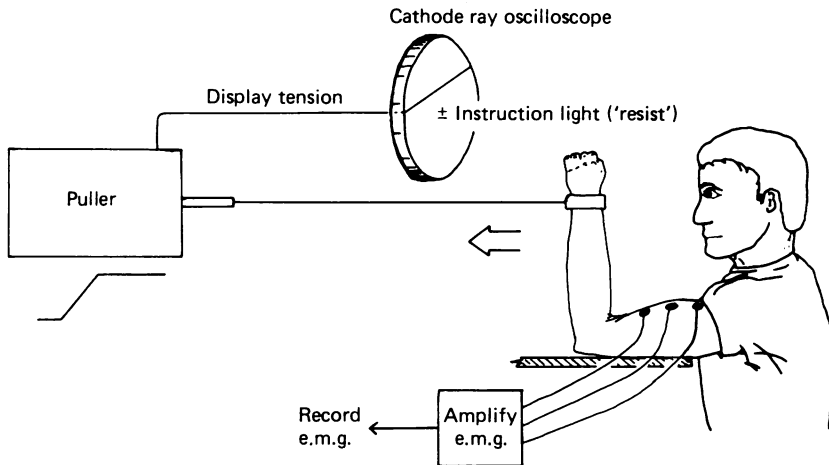


Fig. 1. Schematic diagram of experimental arrangement. See Methods.

Experiments were performed on eight healthy adult subjects of both sexes, including three of the four authors. Several other subjects, including the remaining author, were not included in the study because they could not entirely suppress their long-latency reflexes when given *prior* instruction to 'let go': all but one of these subjects could, however, modify the size of this reflex response without being able to suppress it according to strict criteria (see below). Each subject was seated with his elbows resting on a chest-high table before him (see Fig. 1). The left elbow was flexed at 90°. A leather band was strapped around the left wrist and was connected through an inextensible cable to the shaft of a large electromagnetic vibrator (Advanced Dynamics: AVN 300), which was used to extend the elbow forcibly. The left wrist was rotated so that the plane of the hand ran sagittally: the wrist band thereby came to pull on the tip of the radius. The cable from the wrist band to the electromagnetic vibrator was at 90° to the forearm, i.e. parallel to the upper arm. The vibrator was equipped with positional feed-back, so that the position of the shaft at any time could be monitored. In addition, the magnitude of the motor current required to hold the vibrator shaft at a predetermined position when the subject pulled gently against it gave a signal of the tension achieved by the subject prior to any imposed stretch.

Electromyographic activity was recorded through two surface electrodes placed over the left biceps, with a third electrode placed between these and connected to ground. Biphasic recordings were amplified ( $\sim \times 1,000$ : band pass 50 Hz–10 kHz) and displayed on a storage oscilloscope. They were also fed into an electrophysiological transient recorder (Neurolog NL 750) prior to printing at a slow rate on a pen recorder (Hewlett Packard 1702). Single sweeps of 'raw' e.m.g. activity were recorded, starting 150 msec before the commencement of each forcible extension of the elbow and continuing thereafter for a further 100 msec. An equal level of e.m.g. activity and achieved tension were present in the control periods prior to the stretch.

The electromagnetic vibrator was driven by a ramp generator, and extended the elbow through

7° in a period which was adjusted for each subject (from 50 to 150 msec, average 100 msec) so as to minimize the amplitude of the tendon jerk, or M1, response. Prior to each pull, the subject exerted a gentle isometric tension (~ 500 g) against the vibrator: this tension was kept constant by the waiting subject who was given visual feed-back of achieved tension, and a target line, on an oscilloscope screen. Subjects could observe their e.m.g. responses to each stretch simply by looking across to the experimenters' storage oscilloscope.

For each subject the voluntary reaction time for an e.m.g. response to a tap at the wrist was determined before the responses to muscle stretch were recorded. For this the vibrator was adjusted to deliver a series of brief (~ 2 msec), barely perceptible, taps at the wrist, and the subject was instructed to pull as soon as each occurred. A reaction was scored as soon as peak-to-peak amplitude of recorded e.m.g. exceeded twice its control level. For our subjects, voluntary reaction times in this test all lay between 80 and 95 msec. Nevertheless, because others (Everts & Granit, 1976) have occasionally recorded voluntary e.m.g. reaction times of as low as 70 msec in similar circumstances, we chose to define 70 msec as the boundary before which any evoked e.m.g. activity should be regarded as reflex. Therefore, we regarded long-latency, or M2, responses as those e.m.g. responses occurring *after* 40 msec from commencement of a stretch (i.e. after a monosynaptic reflex latency: here 20–30 msec) but *before* 70 msec (i.e. before a voluntary reaction time): such a procedure was necessary because there was rarely a clear hiatus between M2 and voluntary e.m.g.s.

Recorded responses were scored by an all-or-none criterion: an M2 response was present if the peak-to-peak amplitude of e.m.g. activity exceeded twice the base line level at any time between 40 and 70 msec, and was absent if none of the activity in this period exceeded this level. Correlations were tested between the instructions given to the subjects and the presence or absence of long-latency e.m.g. responses using a  $\chi^2$  test.

## RESULTS

### 1. *Prior instruction*

For each of the eight subjects there were highly significant correlations between *prior* instructions and the presence or absence of reflex e.m.g. responses between 40 and 70 msec from commencement of the pull ( $P < 0.001$ ,  $\chi^2$  test, forty trials). That is, when instructed to 'resist' the subjects could reliably produce a doubling or more of the resting e.m.g. amplitude during this period, and when instructed to 'let go' they could reliably suppress activity through this period (see Fig. 2).

The subjects found it difficult to give an account of the strategies they used to control the long-latency responses when given prior instruction. Some said that they determined to hold the *position* of the arm fixed when told to 'resist', and to permit it to move when told to 'let go'. Others spoke of preparing to pull or to push, as appropriate, when the stretch was applied.

### 2. *Simultaneous instruction*

None of the subjects was able to control the amplitude of the 40–70 msec e.m.g. response according to instructions given at the time the stretch was applied. The correlation between instruction and long-latency response was no better than random (see Fig. 2).

Some subjects showed a tendency to resist, or to let go, for all pulls in quite long sequences, as if the decision to resist or to let go was made and persevered with regardless of the instructions given. Other subjects varied their responses from trial to trial without any demonstrable relation to the instructions given. All subjects expressed frustration in these trials at their inability to control the responses: this

was particularly so for the three authors who were subjects, and who sat for extended sessions trying, in vain, to acquire the ability.

Most subjects were able to maintain a required tension without a reference beam, and were then still unable to control the long-latency reflex when only the instruction light was available. The essential asymmetry of the instruction (light or no light) given in this part of the experiment did not produce any asymmetry of re-

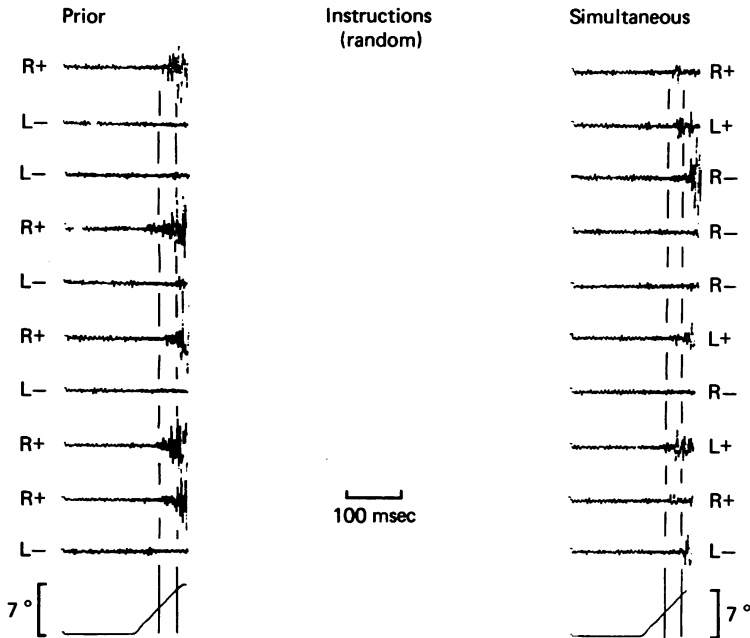


Fig. 2. Records of electromyographic activity recorded from the elbow flexors in one subject. The left-hand panel shows records from ten successive trials when the instruction to 'resist' (R) or 'let go' (L) was given 2-5 sec *prior* to the perturbation which extended the arm through  $7^\circ$  in 100 msec. The right-hand panel shows another series of ten successive trials in the same subject when the instruction to 'resist' was given at the time of the perturbation, by means of a light. Electromyographic activity that exceeded twice the base line level at any time during the period 40-70 msec after commencement of the stretch was scored as a plus (+). If none of the e.m.g. activity within this period exceeded this level, the response was scored as a minus (-). The subject could reliably match his 'long-latency' responses to instructions given prior to a perturbation but not to those given at the time of a perturbation. All eight subjects behaved similarly.

sponse. Approximately equal numbers of long-latency responses were present as were absent. Thus, there was no demonstrable asymmetry in the responses and so the instructions to 'resist' and to 'let go' were effectively equivalent.

When 'simultaneous' instructions were given to two of the subjects through taps at the wrist rather than as lights, the relation between long-latency response and instruction was again no better than random. This form of instruction was not used further when the subjects reported that they could not perceive the wrist taps when

they preceded stretches, even though similar taps were readily perceived when given alone.

#### DISCUSSION

The experiments reported here give no support to the idea that evaluative processes commencing at the time of a perturbation can influence long-latency reflex responses to that perturbation.

In the original formulation of their hypothesis, Newsom Davis & Sears (1970) instructed subjects *prior* to a perturbation that they should 'resist' or 'let go', '*when they perceived the load*'. That the subjects succeeded in modulating long latency reflexes in these circumstances was taken to show at work a mechanism which 'conjoined load perception with servo action' (Sears, 1974). However, in neither Newsom Davis & Sears' experiments nor ours was it necessary for the perturbations to be *perceived* before the long-latency responses could be modified.

Possibly the 'central evaluative processes' through which long-latency reflex modification was achieved may have been unperceived, or at least not-yet-perceived, when that modification actually occurred. We have shown that processing of information which is presented with a load cannot advance far enough to modify a reflex response to that load. It follows that the information relevant to reflex modification such as we have observed must arise before presentation of the load. It seems likely that the signals which are important for such reflex modification are initiated when the decision is made to 'resist' or to 'let go'. It is possibly relevant that alterations in the activity of motor cortical cells occur in response to instructions regarding a forthcoming response, and before the perturbation which will evoke that response has occurred (Evarts & Tanji, 1974; Tanji & Evarts, 1976). By *pre-setting* the excitability levels within the long-latency pathway according to instruction and intent, responses to perturbations could be pre-set: whether or not perception of those perturbations occurs need not then be concerned with the sizes of responses evoked.

An important corollary of the hypothesis of Newsom Davis & Sears (1970) is that the latent period between perturbation and long-latency response allows 'the subsequent phase of reflex action to be matched in sign and intensity to the voluntary movement occurring consequent on perception of the unexpected load' (Sears, 1974). Such matching was not evident in the experiments reported here. In the series of stretches in which simultaneous instructions were given, long-latency reflex responses frequently occurred without subsequent voluntary activity (i.e. e.m.g. responses after 70 msec), and marked voluntary activity frequently occurred without prior long-latency reflex responses. Several instances of this dissociation of reflex and voluntary activity are illustrated in the panel at the right of Fig. 2.

Newsom Davis and Sears' hypothesis was framed in terms of reflex modifications made in response to muscle loading. However, in their experiments and in ours, similar loads were applied and the reflex responses to them were modified by the subjects. The 'central evaluative processes' concerned, therefore, must have involved factors other than just the nature of the load itself.

Our experiments have demonstrated that a visual instruction given at the time

of the load cannot participate in the central evaluative process. The voluntary reaction time to a visual signal exceeds the long-latency response time (Evars & Granit, 1976; our own observations), but this is not relevant to the present study because the possibility being tested concerns modifications achieved before a voluntary reaction can occur. The voluntary reaction time to a kinesthetic or cutaneous signal also exceeds the long-latency response time. As noted in the Results section, attempts to give instructions as kinesthetic or cutaneous inputs failed here because of the subjects' inability to perceive these inputs separately from the applied loads (possibly because of 'backward masking': cf. Matoyan, 1975). These failures make it unlikely that fine discriminations regarding kinesthetic or cutaneous stimuli could be performed, let alone acted upon, within the brief period up to the appearance of a long-latency reflex.

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