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Charles Capaday · Robert Forget · Ted Milner

A re-examination of the effects of instruction on the long-latency stretch reflex response of the flexor pollicis longus muscle

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Abstract We re-examined the issue of how a subject's intention to react to a joint perturbation may modulate the long-latency M2 stretch reflex response. The experiments were done on the flexor pollicis longus muscle (FPL) of the human thumb, for which there is evidence that its M2 reflex response is mediated, at least in part, by a pathway that traverses the motor cortex. The participation of the cerebral cortex in the genesis of the M2 reflex response may allow for a modulation of its amplitude, based on the intention of the subject. To test whether the M2 response is genuinely modulated by the subject's intention, we examined the magnitude of this response as a function of the FPL background level of activation, measured by the surface rectified and filtered EMG. The subject was instructed either to oppose the perturbation as quickly as possible, not to react, or to relax as quickly as possible after the onset of the perturbation. The time integral of the long latency FPL EMG response, computed between 40 and 70 ms following the onset of stretch, was plotted against the mean torque produced by the distal inter-phalangeal joint of the thumb, or against the mean background FPL EMG. There were no significant differences in the FPL M2 EMG responses for different instructions. The amplitude of the reflex response was dependent only - in an approximately linear manner – on the background level of muscle activation. The total joint stiffness (intrinsic plus reflex) was also calculated for each combination of instruction and background torque. This variable was

C. Capaday (\boxtimes)

Centre De Recherche en Neurobiologie, Hôpital de L' Enfant-Jésus, Université Laval, 1401 18° Rue, Québec, Canada G1J 1Z4, FAX no: (418) 649-5910

R. Forget · T. Milner¹ Institut de Réadaptation de Montréal, Université de Montréal, 6300 Darlington, Montréal, Canada, H3S 2J4

Present address:

¹ Department of Kinesiology, Simon Fraser University, Burnaby, BC, Canada V5A 1S6 calculated over a time interval (from 75 to 105 ms) that included the torque due to the M2 reflex response superimposed on the background torque, but was well before any voluntary reaction. Again, there were no significant differences in joint stiffness as a result of the instruction. We therefore conclude that, despite a cortical contribution to the M2 stretch reflex response, this response is not influenced by the intention of the subject on how to react to a perturbation.

Key words Long-latency EMG \cdot Stretch reflex Reflex modulation \cdot Motor cortex \cdot Human

Introduction

Recently, a direct contribution of the motor cortex to the genesis of the long-latency M2 stretch reflex response of two human hand muscles, the flexor pollicis longus muscle (FPL) and the first dorsal interosseous muscle (FDI), has been demonstrated (Capaday et al. 1989,1991; Matthews et al. 1990). Complementary, though indirect, evidence using magnetic stimulation of the motor cortex has also been published (Day et al. 1991; Palmer and Ashby 1992; see Matthews 1991 for a review). Adaptive modification of this response according to the requirements of the motor task may be one of the advantages that a transcortical stretch reflex pathway could provide. This idea was first proposed by Phillips (1969), based on the then newly discovered cortical projection of muscle spindle information. The main experimental paradigm which has been used to test this hypothesis involves determining how the amplitude of the M2 stretch reflex response is modified by the intention of the subject on how to react to the joint perturbation used to elicit this reflex. There have been many reports suggesting that the amplitude of the M2 reflex response, which is intermediate in latency between the monosynaptic stretch reflex response (M1) and the fastest voluntary kinesthetic reactions, depends on how the subject responds to the perturbation (Hammond 1956; Lee and Tatton 1975; Evarts and Granit 1976; Colebatch et al. 1979; Jaeger et al. 1982; Calancie and Bawa 1985; Loo and McCloskey 1985). Thus, it is currently widely accepted that the M2 response is enhanced when the subject resists the perturbation and is reduced when the subject relaxes in response to the perturbation (see Marsden et al. 1983; Prochazka 1989; Rothwell 1987).

Other authors, particularly Rothwell et al. (1980), have claimed that the M2 response is not modified by the instruction given to the subject (see also Thomas et al. 1977; Marsden et al. 1983). Rothwell et al. (1980) provided evidence that the apparent enhancement of the M2 response seen by others may be due to very short reaction times to perturbations whose time of occurrence are predicted by the subjects. Clearly, this issue remains controversial and requires re-examination by an approach that circumvents the potential problems associated with previous studies. The present study improves on the previous ones in two respects. The experiments were done on the FPL of the human thumb, for which there is now strong and direct evidence that its long-latency M2 stretch reflex response is mediated, at least in part, by a pathway that traverses the motor cortex. Secondly, for there to be a genuine modulatory effect on the amplitude of this response, the effect must be independent of the level of ongoing motoneuron pool activity (Capaday and Stein 1987; Stein and Capaday 1988). This is a particularly important point, since the M2 response is known to be strongly dependent on the background level of motor activity (Marsden et al. 1976). Our approach, therefore, was to examine the amplitude of the long-latency M2 stretch reflex response of the FPL as a function of the background level of activity of the FPL with three different instructions to the subject: "resist", "do not react", or "let go". By using the background level of motoneuron pool activity as the independent variable, all extraneous influences (e.g., anticipation) than can modify the background are taken into account. Furthermore, this approach provides quantitative measurements of the dependence of the M2 response on the background level of motoneuron pool activity. In this way, it is possible to dissociate changes of reflex amplitude due to changes in the background from any effect due to the intention of the subject (often referred to as the subject's 'set').

Materials and methods

The subject was seated comfortably in a chair with the right forearm resting on a padded support. The forearm was oriented in a fully pronated position. Both the forearm and the proximal phalanx of the thumb were immobilized to restrict movement to flexion and extension of the distal phalanx of the thumb. The distal phalanx was tightly clamped in a small metal cage attached to the shaft of a torque motor (PMI U16M4). The axis of rotation of the distal phalanx was aligned with the shaft of the motor which rotated in the horizontal plane. The torque motor was powered by a linear current amplifier (Kepco BOP 20–20 M) and could generate a maximum torque of ± 5 Nm.

The EMG activity of the FPL and the extensor pollicis longus muscle (EPL) was recorded using active bipolar, stainless steel, surface electrodes (Liberty Mutual MYO 111) with a bandpass of 45–550 Hz and fixed gain of 4600. The electrode contacts were 3 mm in diameter and spaced 13 mm apart. Before the recording session began, the placement of the electrode over each muscle was determined by observing the EMG activity in response to rapid alternating flexion and extension of the distal phalanx of the thumb.

A linear strain gauge, tachometer and potentiometer coupled to the motor shaft recorded torque, angular velocity and angular position, respectively. Position, velocity, torque and EMG signals were amplified and digitized at a rate of 2000 samples/s.

Experimental procedures

Before the beginning of a recording session, the maximum voluntary isometric flexion torque of the subject was measured. This value was used to calculate torque loads of 7.5%, 15%, 22.5%, and 30% of maximal voluntary contraction (MVC). During the experiment, the subject was required to maintain a cursor within a narrow target window (0.5 deg) while a constant torque load opposed flexion. Once the position had been maintained for a random period varying between 2 and 4 s, the motor produced a servo-controlled 10 deg ramp extension of the thumb. The duration of the ramp was 50 ms (average velocity 200 deg/s). The thumb was held at the new position for 700 ms and then released.

The objective of the experiment was to compare the electromyographic and mechanical responses to the stretch when the subject was instructed, in response to the perturbation, to either react, not react, or let go. Each condition consisted of a combination of one of the four torque loads (or zero load) and one of three instructions: do not react (DNR), react to oppose the stretch as quickly as possible (OPP), or relax as quickly as possible after the onset of the stretch (RLX). A display of the recorded torque after each trial was used to determine if the subject had complied with the instruction. In the case of the DNR instruction, a trial was accepted if the torque remained relatively constant after the transient increase produced by the phasic reflex response. In the case of the OPP or RLX instruction, a trial was accepted if there was a large rapid voluntary increase in torque or a decrease to zero within a short reaction time (<150 ms) respectively. The combination of zero load and the RLX instruction was not used, because the subject was already fully relaxed at the onset of the trial. The same combination of instruction and load was continued until 16 trials had been collected that met the acceptance criterion. The condition was then changed to a new combination of torque load and instruction. Conditions were presented in a predetermined random order which was the same for every subject.

Data analysis

The mean value of the rectified EMG for the FPL and EPL, the mean position, and the mean torque were computed over a 200 ms period prior to the onset of the stretch. The mean onset latency of the M2 reflex response (about 40 ms) in the FPL was determined for each subject. The integral of the rectified FPL EMG reflex response was computed from this point until 70 ms following the onset of the stretch. By using 70 ms as an upper limit, any voluntary or triggered responses were excluded. The peak amplitude of the M2 response was also calculated for each combination of load and instruction. The mean position and mean torque were computed over an interval of the same duration, but delayed by 35 ms with respect to the EMG (to account for the electromechanical delay of muscle). The total stiffness of

The experiments were done on the distal phalanx of the right thumb of six healthy male subjects (ranging in age from 22 to 38 years), one of whom was left-handed. All subjects gave informed consent to the procedure. The experiments were carried out in accordance with the ethical standards of the 1964 Helsinki Declaration.

the distal joint of the thumb in this time interval was computed by dividing the change in torque by the change in position produced by the stretch.

The data obtained from the six subjects for each combination of the five loads and three instructions were first analyzed by using a two factor (load and instruction), repeated measures analysis of variance (ANOVA). The purpose was to first identify which factor(s) had a statistically significant effect on the M2 reflex response. Linear regression analysis was then carried out using the data collected for each subject individually. The background torque was the independent variable and either stiffness, initial EPL EMG, or reflex FPL EMG were the dependent variables. This analysis indicated that subjects co-contracted the FPL and EPL more as the background torque increased. In order to reduce the influence of co-contraction in comparing the FPL reflex EMG across instructions, we divided the range of background FPL EMG levels into five bins of equal width such that each bin contained at least eight trials from each instruction. We then compared the mean values of the FPL reflex EMG for each of the five background levels for one instruction with those of the corre-

EPL (µV)



sponding level for the other instructions. Differences were assessed with a *t*-test for comparison of means. Linear regression analysis was also done on the combined data from all subjects, and the slopes and intercepts were compared for the different instructions.

Results

The main question was whether the instruction given to the subject on how to react to the perturbation has any effect on the amplitude of the M2 stretch reflex response. Our findings are summarized in Figs. 1 and 2. It can be seen in Fig. 1 that the M2 reflex response (between 40 and 70 ms) to stretch of the FPL is essentially the same regardless of how the subject responded to the perturbation. In this particular case, the joint torque immediately after the M2 reflex EMG and just before the burst of voluntary activity is slightly larger in the oppose (OPP) condition (starting at approximately 80 ms in Fig. 1) than in the other two conditions (DNR and RLX). However, this was neither a consistent finding nor statistically significant. In general, the total joint stiffness (intrinsic+reflex) was not modified by the intention of the subject (analyzed by a two-way ANOVA).

A small, but clear reflex response is also present in the EPL in this subject and in all others with a latency similar to the M2 response in FPL (Fig. 1). The responses recorded in the EPL were not due to cross-talk, since no activity was recorded by the same electrodes when the subjects were asked to voluntarily produce large bursts of activity in the FPL muscle. Note also that, in



Fig. 1 EMG responses of the FPL and EPL muscles of one subject to stretch of the tonically active FPL (15% of maximum voluntary contraction) are shown for each of three instructions. The net torque exerted by the interphalangeal joint of the thumb is also shown for each of the three instructions. The results obtained in the OPP instruction are shown as *heavy dark traces*, those obtained in the DNR instruction are shown as *striped traces*, and those obtained in the RLX instruction are shown as *thin light traces*. Note, especially, that the M2 reflex EMG response of the SPL, between 40 and 70 ms following the onset of stretch, is the same regardless of how the subject reacts to the perturbation. Each trace is the average of 16 responses

Fig. 2 Scatter plot of the integrated value (minus background) of the FPL M2 reflex EMG response versus the background level of FPL EMG activity, in each of three conditions. Each point in the scatter plot is the mean of 16 values and is plotted along with ± 1 SD of the mean. Results are from one subject obtained in a single session. Note that the size of the FPL M2 reflex EMG response is tied to the background level of activity in the same way regardless of the instruction. The background level of activity in this graph ranged from zero to 30% of MVC. The mean baseline noise level is approximately 3 μ V in this example

the OPP condition, the subject reacted by co-activating, nearly simultaneously, the FPL and EPL. The average latency of this voluntary activity, generated only when the instruction required the subject to oppose the perturbation, was 107.1 ms (SD 4 ms, n=6 subjects). There was usually a clear change in the EMG activity following the M2 response of the FPL, in all three conditions, which could be identified as the onset of voluntary activity. Finally, note that the amplitude of muscle stretch is identical in all three conditions. Thus, the mechanical input was exactly the same in each condition.

The background level of activity shown in Fig. 1 was 15% of the maximum torque that this subject could generate with the distal interphalangeal joint of the thumb. One of the new approaches taken in this study was to repeat the experiments at several different levels of background activity. The dependence of the M2 reflex response on the background level of activity was, therefore, measured quantitatively. In this way, we could separate the effects due to changes in background activity from any genuine effect of the intention of the subject. The data from one such series of experiments is shown in Fig. 2. The integral of the FPL M2 reflex EMG response, measured between 40 and 70 ms, increased nearly linearly as a function of the mean value of the FPL background EMG level, in all three conditions (Fig. 2). Note that the M2 reflex responses shown in Fig. 2 are at matched levels of the background FPL EMG for each instruction. It can be clearly seen in that figure that the M2 reflex response was tied to the background FPL EMG in the same way regardless of how the subject responded to the perturbation. The results of this graphical analysis were confirmed by a two factor (instruction and load) repeated measures ANOVA. The analysis showed that the background load had a highly significant (P < 0.001) effect on the integral of the M2 response, whereas the instruction did not. The same results were obtained for the peak value of the FPL M2 response. Analysis of the EPL long-latency reflex response showed that it too was strongly affected by the background load (P < 0.001), since the EPL co-contracted with the FPL with increasing load, but there was no effect of instruction on this response.

In some cases, examination of the scatter plots suggested that the reflex response may have begun to saturate at the highest levels of required background torque (e.g., the points near 12 and 14 μ V in Fig. 2). However, at the lower levels of background activity, there was ample scope for an increase in reflex, since the reflex was operating on the increasing portion of the input/output curve.

Finally, we wish to draw attention to the need to strictly control the background level of muscle activation. Failure to do so may lead to the erroneous conclusion that the intention of the subject has a modulatory effect on the M2 reflex response. This point can be demonstrated by comparing the M2 response obtained at zero background torque (and thus nominally zero EMG) in the OPP and DNR instructions. In this case,



Effect of instruction on M2 at zero background load

Fig. 3 The effect of instruction on M2 at zero background load. The bar-error plot represents the average value and standard deviation of the FPL M2 reflex response obtained from six subjects in the DNR and OPP conditions when no background load was present. The M2 response was, on average, 1.6 times larger in the OPP condition than in the DNR condition

the M2 response is indeed significantly larger (approximately 1.6 times) in the oppose instruction (Fig. 3). However, it is clear that in this situation there is no control of the subthreshold membrane potential of the α -motoneurons. For example, the membrane potential may be closer to threshold in the OPP condition than in the DNR condition. The key point of the present study is that when comparisons are made at the same level of activity of the α -motoneurons, as estimated by the mean value of the surface rectified and filtered EMG, the M2 response is not modified by the intention of the subject. Linear regression analysis of the FPL M2 response plotted against background FPL EMG confirmed that there were no significant differences among the slopes of the regression lines for the three instructions. However, the intercept of the OPP instruction was significantly higher than that of the DNR or RLX conditions, as implied by the data of Fig. 3.

Discussion

The purpose of the present study was to determine whether the manner in which a subject voluntarily responds to a joint perturbation has a modulatory effect on the long-latency M2 stretch reflex response of the muscle(s) acting at that joint. The main finding was that the amplitude of the FPL M2 stretch reflex response was strongly dependent on the background level of EMG activity, but was not modified by the intention of the subject. It was clear that any potential effect of the intention of the subject was, at best, quite modest (e.g., Fig. 2). Indeed, our measurements of total joint stiffness (intrinsic + reflex) support this assertion. This variable also measures any potential contribution of the EPL long-latency reflex response (Fig. 1) and the level of FPL-EPL co-contraction at the time of the perturbation.

Methodological issues

Two potential methodological problems may have precluded observation of any effect of the intention of the subject on the FPL M2 response. The first is that the stretch amplitude that was used (10 deg of arc) produced a maximal (saturated) reflex response. The second is that the time window (40–70 ms) used to measure the integral of the FPL M2 response was too narrow to measure a possible increase in the duration of this response, as opposed to an increase of its amplitude.

It is also known that the M2 response increases with the stretch amplitude and duration, as well as with the rate of stretch (Lee and Tatton 1982; Marsden et al. 1983). In any case, as can be seen in Fig. 2, there is ample scope for an increase of the M2 response at low and intermediate levels of FPL activity, but none was observed. Similar arguments can be made against the possibility that our recording electrodes sampled the activity of only a restricted portion of the FPL muscle.

We looked carefully at the averaged records of the FPL M2 response in the three experimental conditions tested to determine if the duration of this response changes. It was not always easy to determine exactly where the M2 response ended, because its termination often blended with the underlying tonic background activity. However, even in these cases, and especially in cases where there is a clear pause after the M2 response, the duration of the response did not appear to be changed by the intention of the subject. In summary, our stringent measurement window excluded potential contributions from short latency voluntary or triggered reactions (Crago et al. 1976), but did not underestimate the magnitude of the M2 response. Further support for this idea comes from our finding that the peak amplitude of the M2 response was also not modified by the intention of the subject. It would be rather surprising if the M2 response were only modulated in duration, but not in amplitude.

Comparison with previous studies

The present results support those of Rothwell et al. (1980), who showed that when the time of occurrence of the perturbation was unpredictable, as in our study, the M2 response was not modified by the intention of the subject on how to react to the perturbation. They suggested that reported increases of the M2 response were due to short reaction times to perturbations whose time of occurrence was predicted (see Rothwell 1987 for further details). Our study extends that of Rothwell et al. (1980) by showing that, at least for the FPL, the manner in which a subject voluntarily responds to a perturbation.

tion cannot alter the size of the M2 stretch reflex response independently of the background level of activity. The amplitude of the FPL M2 response is tied to the level of background activity in the same way, regardless of how the subject responds. On the other hand, it is possible that homologous responses in other muscles (e.g., biceps brachii) may be mediated by neural mechanisms different from those of the FPL M2 response (Thilmann et al. 1991). These authors provided some evidence that the long-latency stretch reflex responses of muscles such as the biceps brachii and the triceps surae may not be mediated by a transcortical pathway, as are those of the hand (Capaday et al. 1989,1991; Matthews et al. 1990). Therefore, in these muscles, the neural mechanisms generating the long-latency stretch reflex responses may be influenced by voluntary activity, but this remains to be shown according to the criteria of the present study.

Our results bear only on the effects of voluntary reactions to a perturbation, on a moment to moment basis. They do not exclude the possibility of long-term changes resulting from specific training procedures (Wolpaw and Carp 1990); changes which may occur within the preparatory time for a voluntary movement (Bonnet 1983), or task-dependent changes (Dufresne et al. 1980; Akazawa et al. 1983; Mackay et al. 1983; Hore et al. 1990; Doemges and Rack 1992). Indeed, in the study of Doemges and Rack (1992) a clear task-dependent change in the amplitude of the M2 response of the FDI was demonstrated, independent of the level of background activity. Task-dependent changes of the monosynaptic reflex (M1) have been shown to occur during natural motor tasks such as standing, walking, and running (see Stein and Capaday 1988; Stein et al. 1991). Taken together with our observations, we conclude that transmission within reflex pathways, including cutaneous reflex pathways (Rossignol et al. 1988; Yang and Stein 1990), is modulated automatically as a function of the motor task, but not directly by the intention of the subject (see also Rothwell 1987).

Implications for neural mechanisms

The present observations have a number of implications for the various possible neural mechanisms through which the M2 stretch reflex response of hand muscles may be modulated. On the input side, the gamma system may modulate the sensitivity of the muscle spindles and thus the discharge of Ia afferents, which are the ones that most likely contribute to the M2 response (Matthews 1989). Centrally, the supraspinal contribution to the M2 response may be modulated at subcortical (e.g., thalamic) and cortical levels. Finally, if part of the M2 response is mediated by a segmental pathway, presynaptic inhibitory mechanisms and changes of interneuronal excitability can attenuate or enhance synaptic transmission between primary afferents and motoneurons. It is clear from the results of the present experiments that none of these potential changes occur, to any appreciable extent, as a result of the intention of the subject on how to respond to a perturbation. Perhaps the most intriguing implication of these results is the lack of effect at the cortical level. It seemed reasonable to think, as many researchers have, that a cortical contribution to the stretch reflex would allow for an influence of the will on a reflex response, but such is not the case. There have been many reports of changes of neuronal activity in the motor cortex as a result of instruction alone, without the occurrence of movement (e.g., Tanji and Evarts 1976; Lecas et al. 1986). These changes in motor cortex neuronal activity have been interpreted as a pre-setting of the neuronal motor apparatus (see Evarts 1984 for a review). However, it should be noted that these changes occur as a result of instructions informing the animal about the parameters (direction, extent, etc.) of the required upcoming movement. In other words, the instructions were directly related to voluntary movements, not to reflex processes. The input-output characteristics of reflexes may thus be set, as discussed above, automatically as a result of the task being executed; in the present experiments, holding the distal phalanx of the thumb in a narrow target zone against a constant opposing load. Therefore, the intent of the subject influences the nature of the voluntary movement in response to the perturbation, but not the reflex responses elicited by this same perturbation. Finally, it may be possible that during such a voluntary movement (i.e., once voluntary activity begins in the OPP condition) the input-output characteristics of the M2 response may be different from those in the DNR or RLX conditions. Some evidence that such a task-dependent transition of input-output properties may occur has been suggested by Soechting et al. (1981).

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