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Self-generated rapid taps directed to the opposite forearm in man: anticipatory reduction in the muscle activity of the target arm

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A brief hammer tap applied passively (by the experimenter) to the forearm elicits a short-latency reflex response in the forearm flexors and extensors. When the same tap is performed actively (by the subject) using the opposite forearm, the reflex response is preceded by a short-lasting anticipatory reduction in the muscle activity appearing around the impact. This anticipatory reduction is interpreted as an alternative mode of feedforward motor control associated with damping of kinetic impulses generated within the bimanual system.

During purposeful manipulations the moving limb segments can be unexpectedly or expectedly perturbed by environmental forces and/or by torque pulses generated within the bimanual system. The compensation of these perturbations requires feedback and feedforward modes of motor control organized at the highest integrative level.

Anticipatory motor actions (feedforward mode of motor control) have already been observed in a broad repertoire of voluntary movements associated with postural adjustments [1–3,8,9]. Preparatory actions have also been established in unimanual and bimanual tasks. The main finding appears to be the association of active unloading of the forearm with anticipatory reduction in the electromyogram (EMG) of the forearm flexor muscles [4] whereas loading is preceded by increased co-activation of the forearm flexors and extensors [5,6].

In contrast to an anticipatory co-activation of the load-bearing muscles, the present work shows that load pulses with a high dynamic component (brief hammer tap) actively applied to the opposite forearm by the subjects themselves are associated with an anticipatory reduction of the tonic activity in the forearm flexors and extensors on the affected side.

All experiments were performed on 17 healthy subjects. During the test, the subjects sat comfortably with

one of both (preferred or nonpreferred) upper arms held in a nearly vertical position, slightly abducted at 20–30°. The forearm was held without any support horizontally with the wrist semisupinated and the elbow joint set at 100°. The subjects, with eyes open, were asked: (a) to perform with one (active) hand a brief hammer tap directed to the radial region of the contralateral (target) forearm; and (b) during the task to keep the position of the target arm unchanged. Alternatively, analogous taps were applied passively (by the experimenter). In both cases, the taps started with the hammer positioned over the target forearm at 10 cm from the target area.

Measurement of changes in the tonic muscle activity preceding the impact was made under the following conditions:

- (1) The hammer tap was performed passively by the experimenter: (a) unexpectedly for the subject; and (b) expectedly for the subject by the use of a time-coincidence task. In the latter, a warning command was followed by three consecutive clicks presented at 1000-ms intervals. The experimenter performed the tap simultaneously with the third click.
- (2) The hammer tap was applied actively by the subject: (a) to the target area of the opposite forearm; and (b) to a target located in the extrapersonal space, 20–25 cm distal to the contralateral hand.
- (3) During an active task (a tap performed by the subject), in 20% of the trials the movement was unexpectedly arrested by a small platform set over the radial region of the hand. Here, the subject, with closed eyes, did not

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know in advance whether the platform was placed over the hand or removed. The experiment started with 10 control measurements (no platform) followed by 50 test trials. During the test, the movement was unexpectedly arrested at least ten times.

The tap was performed by the use of a modified version of a neurological hammer with an incorporated force transducer (Kistler 9311 A). The peak force of the tap was maintained between 20 and 50 N, except when the effects of the intensity of taps were studied (see below); trials with peak forces outside this range were not further processed.

In the individual test series, the number of trials was limited to 50–60 (for further explanations, see below). They were separated into consecutive blocks corresponding to the tests used in the session. Every block comprised equal number of trials (20, 25 or 30 in the different series).

The measurements of the EMG were made by bipolar silver disk electrodes (leading-off area 0.8 cm²) located above the flexor carpi ulnaris of the active forearm and the brachioradialis, biceps and triceps muscles of the target arm. The EMG signals (3 Hz–1.5 kHz) and the force signal (0.002 Hz–1 kHz) were sampled at a rate of 3000 s⁻¹ by a CED 1401 data acquisition system and stored. The EMG data were rectified off-line, averaged and smoothed with a cut-off frequency of 150 Hz. During averaging, each trial was synchronized with the onset of the impact.

A brief tap applied unexpectedly by the experimenter elicited a short-latency reflex response in all forearm flexor muscles of the target arm. This reflex response was not preceded by any significant changes in the EMG even with task manipulations (introduction of warning signals or time-coincidence task) which decreased the time uncertainty of the appearance of the impact (Fig. 2B).

When the hammer tap was performed actively (by the subject), the short-latency reflex responses were preceded by a dramatic reduction in the EMG (Fig. 1). As a rule, this anticipatory reduction could be obtained over all muscles acting around the elbow joint but it was most apparent in the biceps muscle. The anticipatory reduction in the muscle activity (RMA) was observed consistently in the forearm flexors and extensors of the target arm in nearly all (16 out of 17) subjects. During control measurements, it was found that the EMG pattern observed with the subject's eyes opened was similar to that established with closed eyes, indicating that visual information was not important for the appearance of anticipatory RMA.

The anticipatory RMA occurred when: (a) the subject intended and performed the goal-directed rapid move-

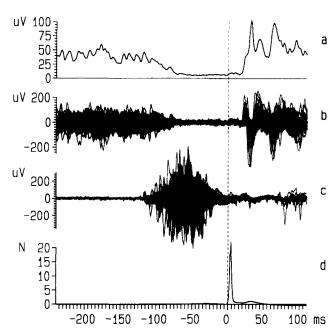


Fig. 1. Anticipatory RMA associated with active hammer tap performed by subject: (a) averaged EMG measured from biceps muscle on affected side (n = 25); (b) raw interference EMG; same data as in Fig. la presented by superposition of single trials; (c) EMG recorded above flexor carpi ulnaris of arm performing tap; and (d) averaged force measured by force transducer of hammer. Vertical hatched line, onset of impact.

ment actively using either the preferred or the nonpreferred arm; (b) the peak force of the impact reached 10–15 N; above this threshold the reduction in the EMG quickly reached maximal values (Fig. 2A); and (c) the active movement was unexpectedly arrested before the hammer hit the opposite forearm (Fig. 3B).

The anticipatory RMA appeared quasi-simultaneously in all forearm flexors and extensors. As was already mentioned, it was most apparent in the biceps muscle. The anticipatory RMA in biceps muscle started 40-140 ms (mean \pm S.D. 81 ± 31 ms) before the impact and the maximum reduction of the amplitude of the rectified EMG signals was 55–90% (mean \pm S.D. 68 \pm 11%) relative to the baseline level (Figs. 1-3). The time interval between the onset of the tapping, measured from the EMG of the wrist flexors and the onset of the associated RMA in the biceps muscle of the target arm varied across subjects between 41 and 164 ms (mean \pm S.D. 120 \pm 44 ms). The anticipatory RMA could be observed until the onset of the reflex response. However, it could last significantly longer if the reflex was not elicited. This can be clearly seen in Fig. 3B (Ba, Bb): the anticipatory RMA occurs even when the active movement is unexpectedly arrested before the hammer hits the target forearm.

It should be noted, that the anticipatory RMA disappeared in the first few trials after the arrested tap. This observation suggests that adaptation could be important

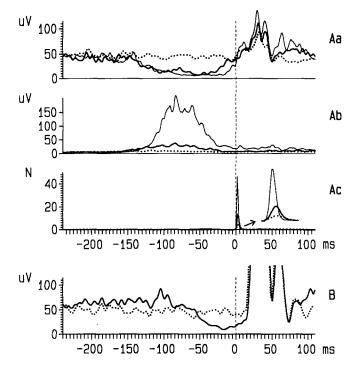


Fig. 2. A: occurrence of anticipatory RMA depending on intensity of impact: (Aa) averaged EMG measured from biceps on affected side; (Ab) averaged EMG recorded above flexor carpi ulnaris of arm performing tap; and (Ac) averaged force measured by force transducer of hammer; arrow indicates same data presented by an expanded time axis. Three data panels (n = 20): dotted line, intensity of tap <10 N; fat solid line, ~15 N; and thin solid line, 45 N. B: averaged EMG pattern from biceps associated with active and passive tap in a time-coincidence task: solid line, subject performs tap quasi-simultaneously (mean \pm S.D. 5.2 ± 17.9 ms) with third click (n = 30); and dotted line, same task performed by experimenter (n = 30, mean \pm S.D. $1.1. \pm 17.5$ ms).

in the development of RMA. Furthermore, if individual series comprised >80–120 trials, the anticipatory RMA decreased or even disappeared. Therefore, changes in the level of attention and concentration should also be taken into account. Thus, the individual series comprised of a maximum of 60 trials.

The anticipatory RMA associated with active rapid arm movement (performed by the subject) is the most intriguing finding in our results. However, similar tapping movements directed to targets located in the extrapersonal space are not accompanied by development of RMA (Fig. 3A).

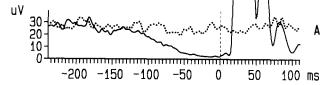
The anticipatory RMA is not a result of body sway with passive elbow flexion caused by the execution of the rapid movement. Participation of interlimb influences transmitted via segmental interneuronal pathways also seems unlikely. The active movement, the amount of the body sway and the elbow flexion should be the same if the target is located either on the opposite forearm or in the extrapersonal space. As was outlined above, RMA

appears only with movement directed to the contralateral arm.

Obviously, the anticipatory RMA is caused by a preprogrammed central command which controls the tonically activated α -motoneurons directly or via the γ loop. RMA does not appear even under predictive situations when the taps are performed by the experimenter (Fig. 2B). Thus, the command providing the development of anticipatory RMA should be integrated in the 'generalized motor program' of the whole bimanual task. This assumes common command center for the bimanual action located in the dominant hemisphere or command centers in each hemisphere with a 'crosstalk' between the two separate pathways [see 7,10]. Such 'crosstalk' would provide coordination of both the command for the tapping movement and the command for the development of anticipatory RMA on the target arm.

It is likely that the preprogramming of the command for anticipatory RMA is based on the experience of preceding events and the associated memory information received by processing of the sensory feedback from muscles, joints and skin. Furthermore, the participation of nociceptive afferents in this preprogramming seems to be less probable because the RMA remains unchanged if a foam rubber is attached to the target area in order to prevent painful stimulation (unpubl. data).

Perturbations unexpectedly introduced during skilled bimanual actions may be compensated for mainly by a feedback mode of motor control whereas undesirable ef-



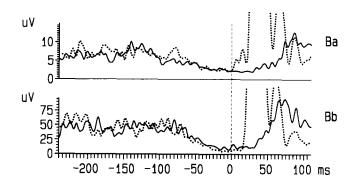


Fig. 3. A: changes in EMG pattern from biceps muscle depending on location of target: solid line, target is on radial region of forearm (n = 30); dotted line, target is located 25 cm far from forearm (n = 30). B: anticipatory RMA when active movement is unexpectedly arrested before hammer hit forearm; averaged results from 10 trials presented by a solid line. Dotted line, controls (n = 10); Ba, EMG from brachioradialis; and Bb, from biceps.

fects of expected perturbations can be eliminated to a large extent via a feedforward mode of motor control.

It is apparent that the anticipatory EMG pattern depends highly on the task conditions. With loading conditions, the preparatory processes can be manifested by increased muscle stiffness due to contraction of the muscles acting towards the directions of the perturbations and/or by co-contraction ensuring postural stabilization of the joints [5,6]. Our results demonstrate a quite different type of feedforward control. With self-generated taps, instead of increased muscle stiffness preceding imposed loading, the expected kinetic pulses are associated with a decrease in the ongoing tonic activity of the forearm flexors and extensors of the target arm appearing around the impact. Consequently, this anticipatory reduced activity implies corresponding decrease in the muscle stiffness. However, the functional role and the mechanisms underlying this anticipatory decreased stiffness remain unclear. One may suggest that the decreased stiffness preceding the impact can serve to dampen the expected kinetic impulses generated within the bimanual system.

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