Mental rehearsal of motor tasks recruits α-motoneurones but fails to recruit human fusimotor neurones selectively

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1. As mental rehearsal of movements activates multiple cortical areas associated with movement, we assessed whether this increases fusimotor drive and whether enhanced muscle spindle activity could contribute to the improvement in skill that accompanies mental rehearsal.
2. Microneurographic recordings were made from six muscle spindle afferents innervating extensor muscles in the forearm or tibialis anterior, which were selected because their discharge increased during very weak contractions. Activity was monitored while subjects imagined performing a range of activities including simple and complex movements involving the relevant muscles.
3. No activation of muscle spindle afferents occurred during imagined motor tasks without EMG. When the relevant muscles contracted during mental rehearsal, spindle discharge increased, much as in weak contractions.
4. Mental rehearsal increased background EMG in the involved muscles and also increased H reflex amplitude independently of EMG changes.
5. Although there was no evidence for selective fusimotor activation during imagined movement, skeletomotor activity and reflex excitability increased. Similar changes occur with preparation for movement following a cue. It is likely that mental rehearsal usually involves unintentional performance of the planned motor task.

Descending pathways from the central nervous system in the cat can activate fusimotor neurones without activity in skeletomotor neurones (e.g. Granit & Kaada, 1952) and may even selectively activate different types of intrafusal muscle fibre (Hulliger, Dürmüller, Prochazka & Trend, 1989; Dickson & Gladden, 1992; Taylor, Rodgers, Fowle & Durbaba, 1992). By contrast, studies in human subjects have suggested that during a range of behaviours (e.g. standing, movement of the fingers) the supraspinal output to fusimotor neurones is closely associated with that to skeletomotor neurones (e.g. Aniss, Diener, Hore, Gandevia & Burke, 1990*b*; Vallbo & Al-Falahe, 1990; for review see Gandevia & Burke, 1992). Limited data suggest that, at rest, there may be background dynamic fusimotor drive to some spindle afferents (Gandevia, Wilson, Cordo & Burke, 1994; see also Ribot, Roll & Vedel, 1986) or that the discharge of some spindle endings can be reflexly modulated without overt EMG (Aniss, Diener, Hore, Burke & Gandevia, 1990*a*; Gandevia *et al.* 1994). However, even with biofeedback training, muscle spindle afferents cannot be recruited voluntarily independently of EMG (Gandevia & Burke, 1985).

Studies using electroencephalographic recording (Weiss *et al.* 1994; Beisteiner, Hollinger, Lindinger, Lang & Berthoz, 1995) and positron emission tomography (e.g. Decety *et al.* 1994; Stephan *et al.* 1995) have revealed that imagination or mental rehearsal of a movement activates many of the central structures which are recruited during voluntary movement, including the motor cortex, supplementary and premotor areas, and cingulate gyrus. These are all regions that contain corticospinal neurones and they should thus be capable of recruiting spinal motoneurones and/or altering reflex excitability within the spinal cord (e.g. Dum & Strick, 1992; Galea & Darian-Smith, 1994). Imagination of movement is believed to enhance subsequent performance (e.g. Feltz & Landers, 1983; Kosslyn & Sussman, 1995), and one scenario would be that it does so by recruiting the appropriate fusimotor neurones and increasing muscle spindle feedback without the interfering effects of muscle contraction. To test this hypothesis we have recorded the discharge of selected muscle spindle endings which were activated in very weak voluntary contractions and examined whether they could be recruited selectively during imagined limb movements. In a second series of experiments we measured EMG and H reflexes during imagined motor tasks, to quantify and compare muscle activity associated with imagined motor tasks to that during control conditions. Mental rehearsal activates muscle spindle afferents but only when α-motoneurones are also activated. These results have implications both for the learning of motor skills and for the interpretation of functional imaging studies of the central nervous system during imagined movement.

METHODS

Studies were conducted on twelve healthy adult males and females aged 19–45 years. The subjects gave informed consent to the experimental procedures which were approved by the appropriate institutional ethics committee. In the first series of experiments, muscle spindle activity was recorded in six subjects from either the radial or common peroneal nerve using standard microneurographic techniques. In the second series of experiments, H reflexes of either the wrist flexors (flexor carpi radialis, FCR) or extensors (extensor carpi radialis, ECR) were elicited by stimulating the median or radial nerve, respectively, and quantitative analysis was made of H reflex amplitude and EMG activity associated with mental rehearsal.

Microelectrode recordings

Subjects were comfortably seated for studies in the upper limb with the arm on a padded adjustable frame abducted 70 deg at the shoulder. For the common peroneal nerve recording, the subject was semi-reclined with the knee flexed 70 deg and the ankle in a padded frame. The limb could be firmly secured to the frame and the force of voluntary contractions recorded using load cells. The postures were chosen because they minimized EMG in the limb. EMG was recorded from the parent muscle with both monopolar needle and surface electrodes (6–10 cm apart) and monitored on a large screen at high gain so that inadvertent contractions could be detected. Gains for the neural and EMG recordings were 20000 (bandwidth, 500 Hz to 5 kHz) and 100000 (bandwidth, 8 Hz to 3·2 kHz), respectively. For the monopolar EMG recordings the bandpass was 80 Hz to 3·2 kHz.

Muscle spindle afferents were identified by their unloading response during maximal twitch contractions produced by intrafascicular stimulation, by responses to pressure applied to the tendon and by responses during voluntary contractions. No attempt was made to separate afferents into putative group Ia and group II muscle spindle afferents. Spikes were initially discriminated with a dual time–amplitude window discriminator (DDIS-1; BAK Electronics, Rockville, MD, USA). Signals were taped for reanalysis using spike-analysis software as previously detailed (Spike2, Cambridge Electronic Design, Cambridge, UK; see Gandevia *et al.* 1994). Only those muscle spindle afferents that were held for more than 30 min (range, 30–90 min; median, 55 min) and which could be activated consistently during very weak contractions of less than 1% of maximal voluntary force were studied. During the microneurographic recordings, an estimate of the surface EMG activity associated with mental rehearsal was made from the number of distinct EMG bursts (i.e. EMG activity >3 times resting level lasting >1 s) during 5 min periods of relaxation and the imagination of movement performance. This measurement is likely to underestimate the number of actual EMG bursts and was not designed to detect minor brief increases in background EMG. Additional more sensitive measures of EMG were made in separate experiments (see below).

Subjects were asked either to relax or to imagine (i.e. rehearse mentally) performing a range of simple and complex activities with the receptor-bearing limb. Each sequence lasted 30–60 s. For all sequences subjects were requested not to move the limb. The first sequences involved imagined weak alternating flexion and extension at the relevant joint (at a level equivalent to about 5–10% of maximal strength), with each phase lasting about 5 s. Subjects were then asked to imagine alternating flexion and extension of increasing strength and speed. The third set of sequences involved imagining complicated activities, which for the upper limb were: conventional handwriting, backward handwriting (i.e. right to left), tracing around imagined symbols (such as a star shape), and threading a needle, and, for the one afferent in the lower limb, walking on a high beam. Finally, subjects had additional periods in which they were free to imagine performance of other self-selected motor tasks.

EMG and H reflex recordings

In the second series of experiments, the level of EMG associated with mental rehearsal was further quantified. Two pairs of surface electrodes with inter-electrode distances of 4 cm were placed to record EMG activity from wrist flexors (FCR) and extensors (ECR). The EMG was recorded at high gain (×50000–100000; bandpass, 16 Hz to 3·2 kHz). In preliminary trials, subjects received auditory feedback of the EMG, but no feedback was given during the recorded trials, and the average level of rectified EMG in the 50 ms immediately prior to each H reflex stimulus was measured for both the flexor and extensors of the wrist.

H reflexes were elicited with stimuli of 1 ms duration delivered at 0·1–0·2 Hz to the radial nerve in the spiral groove (ECR) or to the median nerve at the elbow (FCR). The H reflex for each muscle was studied on two separate occasions for each individual but, if H reflexes were not detectable at rest (i.e. with no background EMG), the session was terminated. H reflexes in ECR (10 subjects) or FCR (4 subjects) were recorded in sets of ten, while the subject performed specific tasks. For each subject, up to 600 H reflexes (from either ECR or FCR) were measured in the two recording sessions.

During trials of deliberate relaxation, the subjects were asked to focus on the test limb and keep it still and relaxed. In addition to the tasks used when recording muscle spindle activity, reflexes were also elicited during a range of conditions designed to control for the level of subject arousal including: relaxation with constant verbal instructions to be relaxed, quiet reading, reading aloud, mental arithmetic, and deliberate contraction of the equivalent muscle in the contralateral limb. To control for EMG activity, reflexes were also elicited during deliberate weak contractions of the test muscle.

Prior to all mental rehearsal tasks subjects received verbal instructions to keep the test limb still while they imagined performing the required tasks. These included continuous isometric contraction of the test muscle of weak or moderate strength (5–10 and 30–50% of maximum, respectively), alternating wrist flexion and extension (5 s each) of constant strength (either weak or moderate), writing their name (either backwards or forwards) or tracing imaginary five-pointed stars (with particular attention to forming neat letters and symbols).

Statistics

The frequency of bursts of EMG when relaxed and during imagined tasks were compared with Student's two-tailed t test. The amplitudes of H reflexes measured under control and test conditions were compared using analysis of variance. Because the size of the H reflex increases markedly with small levels of background contraction, the levels of background EMG in the agonist (and antagonist muscles) were included as covariates in the analysis. Statistical significance was set at the 0·05 level. Unless indicated otherwise values are given as means ± S.E.M.

RESULTS

Muscle spindle afferent recordings

The discharge of the six spindle afferents (5 from wrist or finger extensors, 1 from tibialis anterior) was recorded during relaxation, imagined contractions of the parent muscle (e.g. wrist or finger extension) and imagined natural movements in which the muscle would usually contract (e.g. handwriting, walking). Mental rehearsal of simple and complex movements was studied for each afferent (see Methods). Two units had a background discharge (7 and 13 Hz), and the remaining four afferents were silent at rest. All six were activated during weak voluntary contractions (< 1% of maximum). Two units without a background discharge at rest developed a resting discharge following weak voluntary contractions, further evidence that their discharge during the contraction was due to increased fusimotor drive (see Wilson, Gandevia & Burke, 1995).

Figure 1 shows data for a unit in extensor digitorum communis. It had no background discharge but was activated during deliberate extension of the fingers (panel *C*). Despite the presence of EMG, the unit was silent during imagined movements of the hand, including handwriting. However, when imagined activity was accompanied by the greater muscle activity that usually accompanied mental simulation of stronger contractions, it and other muscle spindle afferents began to discharge. Figure 2 shows data from a muscle spindle afferent with a background discharge innervating ECR. Small increases in torque and EMG activity were recorded during imagined extension of the wrist. The afferent was activated during the unintentional contraction which accompanied imagined wrist extension. These changes in EMG and force occurred despite the instruction to the subject not to move the limb. Each muscle spindle afferent also discharged with inadvertent contractions which sometimes occurred during the control periods of relaxation.

Figure 3 shows data for a tibialis anterior unit which failed to discharge during a wide range of imagined tasks including ankle dorsiflexion and walking on a high beam, even though liminal EMG occurred during the task. Overall,

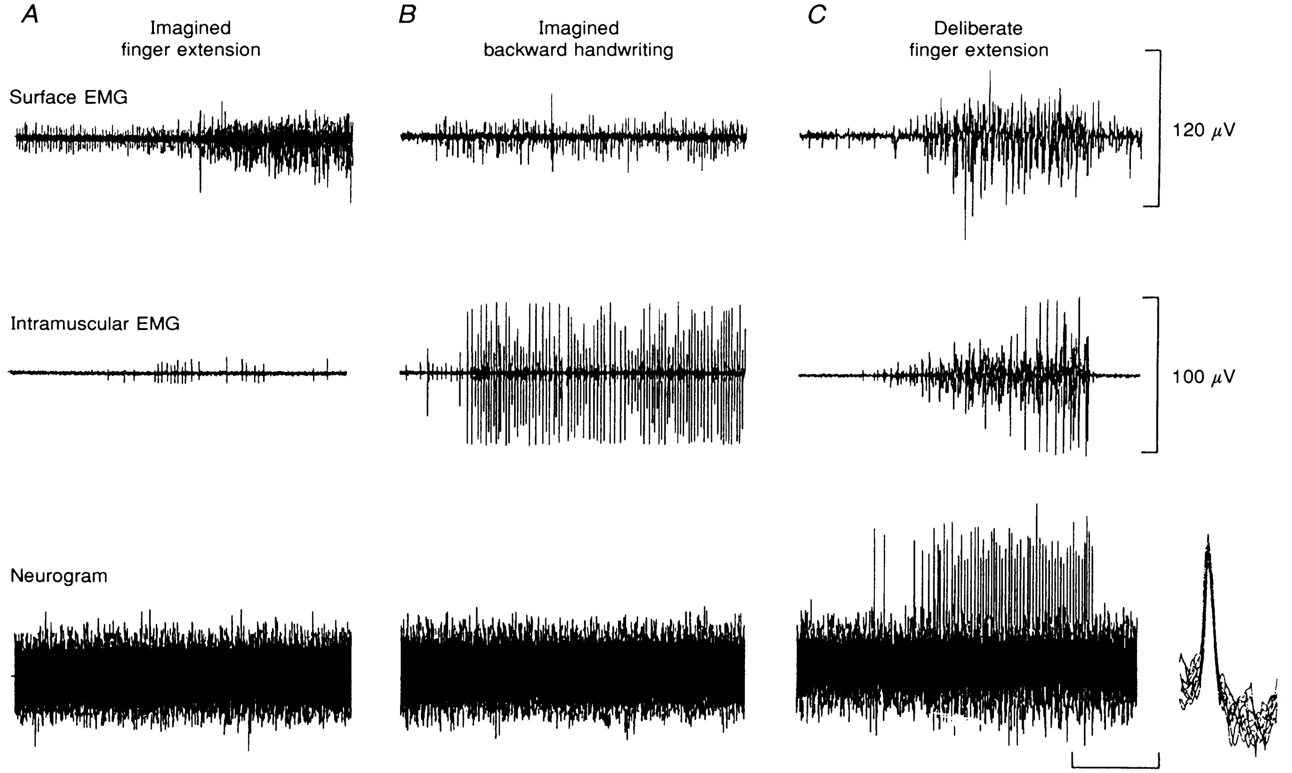

Figure 1. Muscle spindle afferent innervating extensor digitorum communis

A–C, recordings during imagined tasks and deliberate weak finger extension. Traces from the top represent surface EMG, intramuscular EMG, and neurogram, respectively. The inset shows superimposed single-unit action potentials. Horizontal calibration for *A*, *B* and *C*: 4, 3 and 1 s, respectively.

the major finding was that none of the spindle afferents was recruited selectively or increased its discharge without evidence of EMG in the parent muscle during imagined movements. Although not studied formally, the spindle afferents appeared to increase their discharge at similar low levels of EMG during imagined movements and deliberate contractions. This was difficult to document precisely due to the low levels of EMG at which recruitment occurred.

During mental rehearsal the occurrence of overt bursts of EMG (> 1 s duration; see Methods) increased from 1·0 ± 0·2 to 2·1 ± 0·3 bursts min^{-1}. This trend was present in all subjects and was statistically significant for the group ($P = 0{\cdot}034$). EMG bursts were more prominent with faster and stronger imagined efforts. This definitely links the occurrence of EMG bursts to the act of rehearsing the movements. Given the difficulty in definition of EMG bursts in muscles that were intended to be at rest (see Methods), the effect of imagination on background levels of EMG was investigated quantitatively in the second series of experiments.

EMG

Background levels of EMG were measured during imagination of movements while H reflexes were elicited. The average rectified EMG activity in the agonist muscle (measured for the 7 subjects over the 50 ms immediately prior to each H reflex stimulus) increased significantly during imagined motor activity for the group of subjects ($P < 0{\cdot}001$). When H reflexes of ECR were elicited, the EMG in *both* ECR and FCR increased during mental rehearsal, by a mean of 76 ± 20 and 29 ± 20%, respectively, above the level when the subjects were relaxed. This increase was significant for five of the seven subjects. During testing of the H reflex in FCR, the increases in EMG were 59 ± 58 and 40 ± 17% in ECR and FCR, respectively.

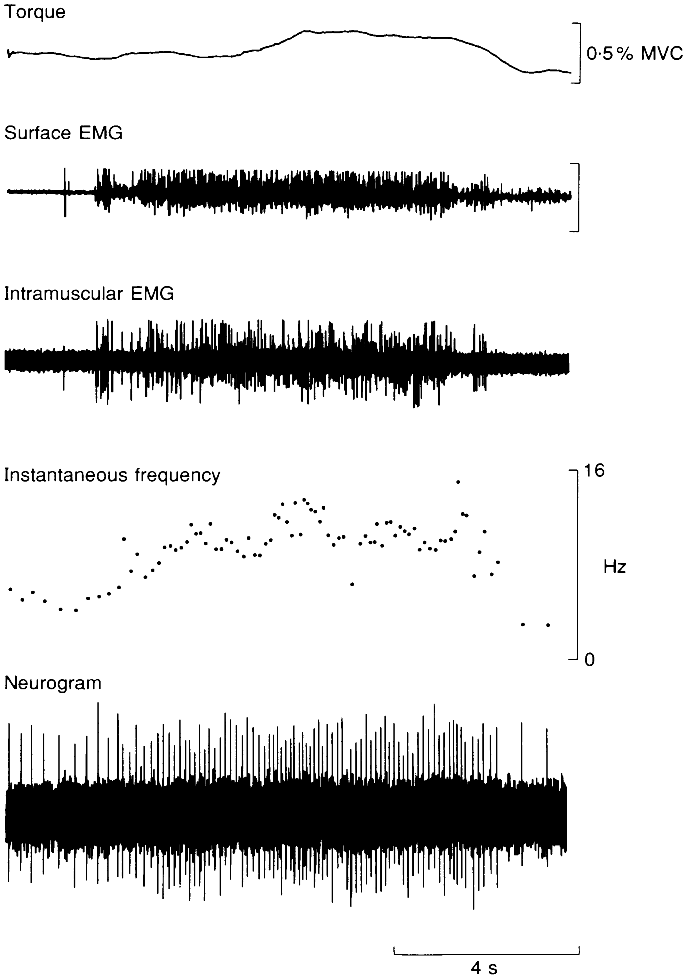

Figure 2. Muscle spindle afferent innervating extensor carpi radialis with increased discharge during imagined wrist extension

Data from a spindle afferent with a resting background discharge rate of 7 Hz. Traces from the top are torque, surface EMG, intramuscular EMG, instantaneous discharge rate of the spindle afferent, and the neurogram. There is some clipping of the surface EMG record owing to the high gain. Vertical calibrations for surface and intramuscular EMGs: 35 and 200 μV, respectively. MVC, maximal voluntary contraction.

H reflex recordings

H reflexes in ECR could be recorded at rest in two recording sessions in four of ten subjects and in only one session in an additional three subjects. In sessions in which the H reflex of ECR could not be obtained reliably when the subject was relaxed, no data on the effect of imagination were collected. When relaxed, mean H reflex amplitudes in ECR were $4{\cdot}5 \pm 3{\cdot}4\%$ of the maximal motor response (mean ± S.D.). H reflexes in FCR were more consistent, being present at rest in both recording sessions for all four subjects (mean, $14{\cdot}5 \pm 5{\cdot}7\%$ of maximal motor response).

Pooled data for H reflexes elicited in ECR for all seven subjects with consistent reflexes at rest are summarized in Fig. 4. The mean increases in H reflex amplitude are plotted

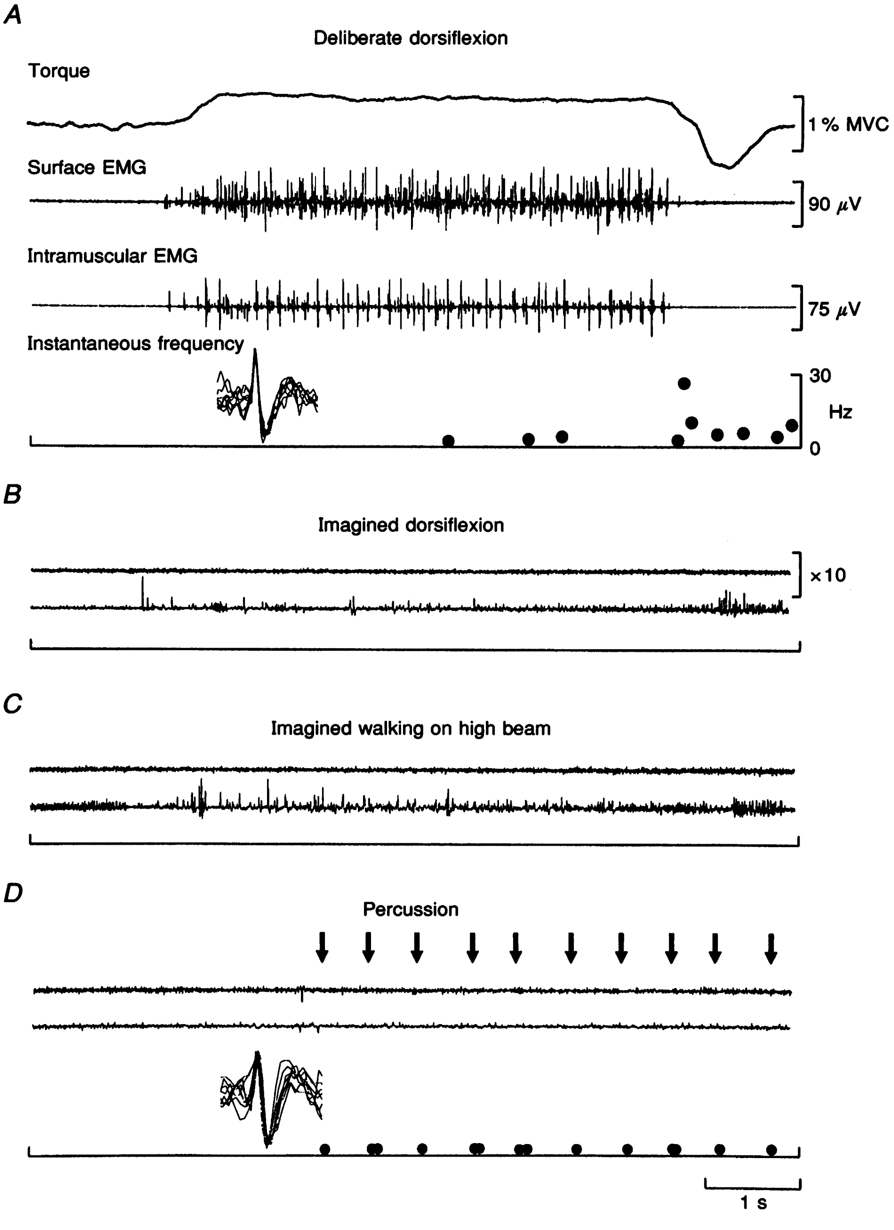

Figure 3. Muscle spindle afferent innervating tibialis anterior

A–D show successive recordings, with traces from the top in each panel representing isometric torque (*A* only), surface EMG, intramuscular EMG, and instantaneous discharge frequency. In *B–D*, the force trace (Torque) is omitted, and EMG gains increased 10-fold. *A* shows the muscle spindle afferent discharging during a weak voluntary isometric contraction and on relaxation. *B* and *C* show imagined weak dorsiflexion of the ankle. Despite liminal EMG detected with intramuscular electrodes, the muscle spindle afferent did not discharge during imagined manoeuvres. *D* shows the subsequent discharge of the muscle spindle afferent (●) in response to repetitive tendon percussion (arrows), indicating that the recording site was maintained throughout the records shown in *B* and *C*. Insets show superimposed action potentials for the panels illustrated.

against the increase in the mean level of background extensor EMG (both expressed as a percentage increase above the mean levels during relaxation) for the range of test conditions. This figure confirms the tendency for increasing levels of background EMG activity to occur in addition to increases in amplitude of the H reflex with imagined motor tasks. A similar result was observed when the wrist flexors were studied. In an additional analysis, H reflexes were compared for matching levels of background EMG, and were slightly, but significantly, greater for 'imagined' trials than for control trials (by ~10–15%, $P < 0{\cdot}05$). Analysis of variance, based on data from individual subjects, confirmed that the amplitudes of both the ECR H reflex and the FCR H reflex increased during mental rehearsal, independent of the confounding influence of changes in the background EMG of the wrist muscles (i.e. some of the increase in the H reflex did not depend on the altered levels of EMG at the time the reflexes were elicited; analysis of covariance, $P < 0{\cdot}001$). As is apparent from Fig. 4, the increase in H reflex amplitude with the imagined tasks was small compared with that during deliberate weak contractions.

DISCUSSION

Muscle spindle discharge is not turned on independently of skeletomotor outflow during imagination or mental rehearsal of movements. Two of the six muscle spindle afferents had a background discharge, and all were recruited or increased their discharge during very weak voluntary contractions, presumably reflecting a significant increase in fusimotor drive with minimal effort. Hence such afferents should be susceptible to small changes in α–γ balance. Although it remains possible that the motor circuits activated by imagination of limb movements might activate fusimotor neurones selectively, any such activation was insufficient to change muscle spindle discharge. Given that there was no overt movement during mental rehersal, any 'subthreshold' activation via dynamic fusimotor neurones is unlikely to be functionally important. Accordingly, an improvement in motor performance due to mental rehearsal of movement is unlikely to be due to enhanced muscle afferent feedback independent of EMG.

Mental rehearsal did activate α-motoneurones and, if this unintended contraction was sufficiently strong, the skeletomotor discharge was accompanied by recruitment of spindle afferents. Since motor units and muscle spindle afferents were commonly recruited with mental rehearsal, the results imply that any improvement in performance produced by imagination (Feltz & Landers, 1983; Kosslyn & Sussman, 1995) could actually be due to subliminal (unintended) performance of the movement rather than merely its mental rehearsal. Accordingly, the situation could be analogous to that when subjects overtly practice the task to be learnt, a situation in which there is no evidence of enhanced or disproportionate fusimotor drive (Vallbo & Al-Falahe, 1990). It is also possible that inadvertent contractions during mental rehearsal and the resultant

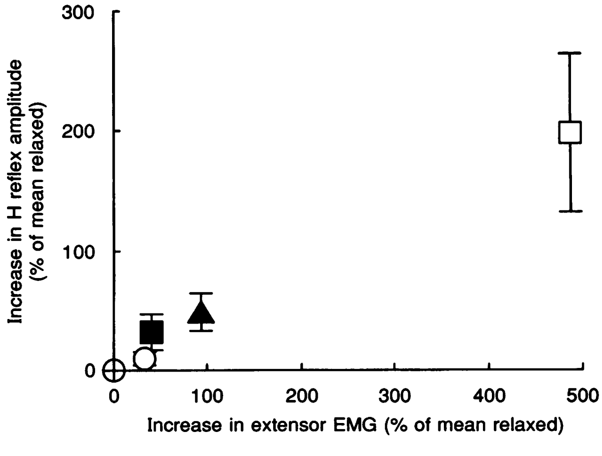

Figure 4. Relationship between increased background EMG and increased H reflex size for a range of tasks

Pooled results for all subjects ($n = 7$) with an H reflex in ECR at rest. Increases in mean H reflex amplitude (± S.E.M.), expressed as a percentage of the mean H reflex amplitude during the task of deliberate relaxation, are plotted against the increase in the mean level of background EMG in ECR, expressed as percentage of mean level of background extensor EMG at rest during deliberate relaxation. Open symbols depict data for control tasks: ⊕, relaxed condition; ○, control tasks other than deliberate relaxation (i.e. mental arithmetic, reading and deliberate contractions of wrist extensors in the contralateral limb; i.e. conventional reflex reinforcement); □, data for a weak voluntary isometric contraction of wrist extensors. The filled symbols represent the tasks involving mental rehearsal: ▲, handwriting; ■, wrist extension. The data highlight the large increase in H reflex amplitude with voluntary contractions and only slight increases in the H reflex with imagination of movement (or with reflex reinforcement).

sensory feedback could contribute to the activation of 'motor' cortical areas revealed by neuroimaging and encephalographic studies. Analysis of data from a recent study using positron emission tomography suggests that small phasic forces, well below 5% of maximum, would be sufficient to 'activate' primary motor and sensory cortex along with other 'motor' cortical areas (see Fig. 4 in Dettmers, Ridding, Stephan, Lemon, Rothwell & Frackowiak, 1996; see also Dettmers *et al.* 1995).

There are theoretical reasons why the presence of small contractions of relevant muscles produced by mental rehearsal may aid the development of motor performance. During voluntary movements, subjects have access to kinaesthetic signals of commands being delivered to muscles and signals related to the actual lengths of, and intramuscular forces developed by, muscles (for review see Gandevia, 1996). While subjects can recruit motoneurones and grade motoneuronal output in the absence of muscle afferent feedback (e.g. Gandevia, Macefield, Bigland-Ritchie, Gorman & Burke, 1993), this ability is improved with auxiliary feedback which signals that the motor command has successfully recruited motoneurones. During mental rehearsal, the feedback produced by liminal contractions presumably involves both spindle and tendon organ afferents and provides a mechanism for perceived motor commands to be linked to contraction of particular muscles. Furthermore, with mental rehearsal this association can be developed when the afferent signals are simple and unaffected by the large changes in muscle length and force during real movements.

The presence of augmented H reflexes independent of altered skeletomotor activity during imagination of movements implies that mental rehearsal can activate descending inputs to spinal reflex circuits. Changes in spinal reflexes are well documented prior to deliberate movement in the absence of EMG (Kots, 1969; Gottlieb, Agarwal & Stark, 1970; Coquery & Coulmance, 1971; Pierrot-Deseilligny & Lacert, 1973), and this rather than enhanced fusimotor drive probably constitutes the mental set associated with the preparation for movement. The present findings are similar to the changes that occur when subjects are provided with a warning that a stimulus to which they must respond is imminent (Burke, McKeon, Skuse & Westerman, 1980). 'Anticipation' is associated with changes in gain of spinal reflexes (Burke *et al.* 1980; Gerilovsky, Struppler, Altmann & Velho, 1983; Frank, 1986; Yamamoto & Ohtsuki, 1989) and muscles are often tensed unintentionally in preparation for the command signal to move. There is, however, no evidence that anticipation activates fusimotor neurones selectively or preferentially as a means of priming central circuits prior to the need to move (Burke *et al.* 1980; Gerilovsky *et al.* 1983), much as is the case with mental rehearsal of movement.

Overall, these findings support the concept that relaxation, imagination and action are a continuum, consistent with Carpenter's idea (Carpenter, 1881) that imagined movements produce qualitatively similar, but quantitatively lesser, drive to muscles than overt movements.

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