Postural after-contractions in man attributed to muscle spindle thixotropy

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1. It is an old observation that non-volitional arm abduction movements accompanied by a sensation of arm lightness often occur as an after-effect following forceful voluntary arm abductor contractions against a restraint. In the present study we have tested the hypothesis that such non-volitional, so-called 'postural after-contractions' are tonic reflex responses to an enhanced resting discharge in primary muscle spindle afferents which in turn is a consequence of thixotropy-dependent enhanced stiffness of intrafusal muscle fibres.
2. Results obtained in ten volunteers show that the arm abductor after-contraction phenomenon in man is most readily evoked by a type of conditioning procedure which in various respects mimics the procedure proven in animal experiments to be particularly effective in producing thixotropy-dependent excitation of primary spindle endings.
3. It is also shown that changes in arm abductor intramuscular temperature affect the strength of the after-contractions in a direction predicted by the thixotropy hypothesis.
4. Attention is drawn to several similarities between the after-contraction phenomenon with accompanying sensory illusions and the tonic reflex responses and illusions that can be induced when primary spindle endings are excited by muscle vibration.
5. The results support our hypothesis that postural after-contractions are induced by activity in primary muscle spindle afferents as a consequence of thixotropic properties of intrafusal muscle fibres. Central excitability changes following the conditioning voluntary effort may contribute to the phenomenon.

The term 'postural after-contractions' stands for a motor (and perceptual) phenomenon in man which attracted considerable scientific interest in the early part of this century but which then has been more sporadically dealt with in the literature. A well-known example of the phenomenon – commonly used as a parlour game amusement – is the following: the subject, standing in a doorway, abducts his arms for a while forcefully against the door posts; when he then relaxes and lets the arms slowly return to their initial position he experiences a transient sensation of lightness while the arms start to rise again due to a non-volitional contraction of the arm abductor muscles. In the old literature divergent hypotheses were presented regarding the neural mechanisms responsible for such after-contractions (Kohnstamm, 1915; Salmon, 1916; Pinkhof, 1921; Sapirstein, Herman & Wallace, 1937; Hick, 1953). A more recent attempt to explain the phenomenon in neurophysiological terms was made in a review article by Granit (1972). With reference to the evidence of α–γ-co-activation in voluntary contractions (Hagbarth & Vallbo, 1968, 1969; Vallbo, 1970, 1971) he attributed postural after-contractions to so-called 'post-tetanic potentiation' of the α-motoneurones following the muscle spindle activation during the largely isometric voluntary effort preceding the after-effect. He also drew attention to certain similarities between postural after-contractions and tonic vibration reflexes. In reports published during the last decade opinions diverge as to whether after-contraction phenomena are primarily due to central excitability changes (Gilhodes, Gurfinkel & Roll, 1992) or to lasting after-discharge from muscle spindles (Hutton, Kaiya, Suzuki & Watanabe, 1987).

The studies on muscle spindle 'thixotropy' during the last decades have now advanced far enough to warrant a new attempt to seek the prime cause of postural after-contractions. These studies, reviewed by Proske, Morgan & Gregory (1993), indicate that, in a similar way as for the extrafusal muscle fibres, the inherent stiffness or slackness of the intrafusal muscle fibres at any given time is highly dependent on the immediate previous history of movements and contractions. This so-called 'thixotropic' behaviour of the intrafusal fibres, explained in terms of formation and disruption of cross-bridges between actin and myosin filaments, in turn affects the excitability and resting discharge of primary muscle spindle endings. Of particular interest in the present context is the observation in the cat that an intrafusal contraction at a short muscle length as a rule is followed by a period of enhanced resting spindle discharge after the muscle has been brought back to the initial intermediate test length (Gregory, Morgan & Proske, 1988).

In the present study on human arm abductor muscles we have tested the hypothesis that postural after-contractions are tonic reflex responses to thixotropy-induced temporary enhancements in the resting firing rate of primary spindle afferents. As judged by the animal studies conditioning procedures involving the following four sequential steps are particularly effective in producing an after-effect of enhanced intrafusal stiffness with an accompanying rise in resting spindle discharge. (1) The muscle is brought from an intermediate to a short length. (2) With the muscle held at the short length the γ-fibres are activated to produce intrafusal contractions, thereby eliminating slackness by detaching cross-bridges adapted to the preceding intermediate length. (3) After contraction, the muscle is held at the short length for a few seconds to promote the formation of cross-bridges adapted to this length (Gregory *et al.* 1988). (4) The muscle is then slowly brought back to the intermediate length. A brisk stretch should be avoided since it is likely to act as a stirring force which detaches the cross-bridges formed at the short length (Proske *et al.* 1993).

The primary aims of the present study were to explore whether conditioning procedures which fulfil these requirements are also particularly effective in producing postural after-contractions, and to examine whether changes in intramuscular temperature can affect the strength of the phenomenon. The rationale for the latter part of the study is that experiments on isolated frog muscle fibres (Buchthal & Kaiser, 1951) and on intact human forearm muscles (Lakie, Walsh & Wright, 1986) have shown that passive muscle stiffness can be reduced by warming and enhanced by cooling, effects attributed to temperature-dependent changes in muscle thixotropy. In addition to these quantitative studies, descriptive comparisons were made between postural after-contractions and tonic vibration reflexes.

METHODS

Subjects

Fourteen healthy volunteers (12 males and 2 females, aged $31{\cdot}4 \pm 13{\cdot}0$ years, mean $\pm$ s.d.) were studied. Prior to the protocolled experimental sessions all subjects passed a test in which they were exposed to the bilateral so-called ‘control type of conditioning procedure’, which (as described below) was designed to fulfil the requirements referred to in the Introduction. In this preliminary test four subjects differed from the others in that they exhibited no apparent signs of any arm abductor postural after-contractions. These four ‘non-responders’ were excluded from the experimental sessions in which a control response was needed to evaluate eventual response reductions in trials where the alleged conditioning requirements were not fulfilled. The study was approved by the local ethics committee and the subjects gave their informed consent.

Mechanical arrangements

Our ‘door post construction’ consisted of a frame with two vertically placed stands firmly fixed at a distance of 90 cm from each other. With the subject standing in the middle between the two stands the extended arms had to be abducted up to an angle of about 20 deg before the dorsum of the hands reached up to the stands (the exact angle depending on the height and the shoulder width of the subject). The arrangements were such that the stands could be removed from the subject to allow free arm movements after completion of the conditioning procedure.

Measurements of arm movements

The goniometers measuring ab- and adduction movements of the arms consisted of potentiometers fixed to the ends of a splint which was adjusted in length to match the shoulder width of the subject. The splint was firmly attached to the chest of the subject in such a way that the rotation axes of the potentiometers were centred to the axes of the scapulohumeral joints. The potentiometer rotation axes were connected to securely fastened arm splints reaching down to the elbows. A minor, unavoidable drawback was that respiratory chest movements were often reflected as low-amplitude oscillations in the goniometer traces. For similar technical reasons small downward drifts in the goniometer traces occurred when the subject unintentionally lifted the shoulders during the forceful abductor contractions (see Fig. 1*A*).

Electromyography (EMG)

Arm abductor EMG activity was recorded with a pair of surface electrodes (Blue Sensor, F-10-Vs, Medicotest A/S, Ølstykke, Denmark) placed 4–5 cm apart over the deltoid muscle. To obtain a mean voltage EMG the amplified signal was full-wave rectified and passed through an ‘integrator’ with an exponential decay time constant of 0·1 s.

Pilot studies showed that as indicators of the strength of the postural after-contractions the deltoid EMG signals were less reliable than the goniometer signals which showed the amplitude of the abduction movements. Slight asymmetries in the positioning of the EMG electrodes could easily give a false impression that the after-contractions were not of equal strength in the two arms, although the arm abduction movements were similar. It also remained uncertain to what extent contractions in the supraspinatus muscle contributed to the arm abductions. For these reasons we decided to omit the EMG recordings from the experimental protocols in the quantitative bilateral trials (see below). However, deltoid EMG recordings were used when studying the effects of voluntary background contractions on the after-contraction phenomenon and when searching for evidence of enhanced extrafusal stiffness following the conditioning procedures.

Cooling and warming of shoulder region

All experiments were performed at a room temperature of 21–23 °C. To change the temperature of the arm abductor muscles, cold – or hot – packs (Coldhot pack, 3M, Medical Products Division, St Paul, MN, USA) were applied over the shoulder region. In pilot tests with a thermosensitive needle probe inserted into the middle of the deltoid muscle belly it was found that 10 min of pack application (with a thin cloth to protect the skin) was sufficient to lower or raise the intramuscular temperature by about 3–4 °C. After bag removal it took about 10 min until the temperature had returned to the initial level of 36–37 °C, a time fully sufficient to examine the effect of the temperature change on the after-contraction phenomenon.

Control type of conditioning procedure

The following type of conditioning procedure consisting of four steps was designed to mimic the procedure which in animal experiments has been found to be particularly effective in producing an enhanced resting discharge in primary muscle spindle afferents (see Introduction). The blindfolded subject stood in the middle between the two stands with the arms initially held in a slightly abducted position (about 3–7 deg from the natural resting position during relaxation). The arms were then actively lifted up against the stands (step 1) and after contact they were forcefully pressed against the stands for 5–10 s (step 2). The strength of the contractions was not measured, but the instructions were to use maximal force. The subject was then told to relax while the experimenter held the arms against the stands for another 4–8 s (step 3). Finally, in the succeeding 3–5 s the arms were passively lowered by the experimenter back to the initial slightly abducted position (step 4), where the subject was instructed to hold them just as before the conditioning procedure.

The instructions to the subjects were that after the conditioning procedures they should try to avoid all active interference with any arm movements that they might perceive as non-volitional.

Experimental protocol

Pilot experiments showed that in a given subject the postural after-contractions, measured as arm abduction movements, were largely symmetrical but varied considerably in amplitude from one trial to the next, although the same control conditioning procedure was used. To reduce the influence of such variations on the statistical evaluation we therefore decided to use a protocol in which each trial consisted of a bilateral test in which the conditioning procedure for one of the arms (the so-called 'test arm') in some specific pre-determined way differed from the control type of procedure for the other arm. The experimental protocol included a *bilateral control type of conditioning procedure* **(trial A)** and the following four types of deviations from this procedure:

Trial B, omission of step 1. The subject was standing not in the middle between the two stands but so close to the test arm stand that, when held in the initial slightly abducted position of 3–7 deg, the test arm could be forcefully pressed against the stand without the arm first being lifted up to a more abducted position. After the forceful isometric contraction the subject did not lower the arm but tried to maintain the same slightly abducted position as before. Thus, in contrast to the control arm conditioning procedure, the test arm conditioning procedure did not fulfil the arm abductor 'hold-short' requirement.

Trial C, omission of step 2. Both arms were in a similar way abducted up against the stands, but while the control arm was forcefully pressed against the stand for 5–10 s the test arm abductor contraction was just sufficient to maintain the abducted position.

Trial D, omission of step 3. In contrast to the return movement of the control arm, which started after 4–8 s of relaxation, the return movement of the test arm was started immediately after the forceful contraction.

Trial E, fast return movement in step 4. The arm return movement (performed by the experimenter) was 5–10 times faster in the test than in the control arm.

The five types of trials described above were carried out in a random order and were separated by rest periods of at least 2 min. The choice of test arm (right or left) alternated from one subject to the next.

Trials were also performed in which, prior to a bilateral control type of conditioning procedure, the test arm was exposed to either *shoulder cooling* or *shoulder warming* (as described above). These trials, which were separated by a recovery rest period of at least 15 min, were performed at the end of the above-described experimental sessions, or as separate experiments.

Analytical equipment

The goniometer and EMG signals were fed into a digital waveform analyser (Data 6100, Data Precision, Danvers, MA, USA) connected to a plotter. When the peak amplitude of the abduction movements was calculated, measurement errors due to the respiration-induced oscillations in the goniometer traces were avoided by setting the cursors at the estimated mid-level of such oscillations.

Statististical analysis

Results are expressed as means ± s.d. For each type of bilateral trial, the angular movement of the test arm and the corresponding control arm movement were compared using Student's two-sided paired t tests with Bonferroni correction for multiple comparisons. The chosen level of significance was $P < 0.05$.

Muscle vibration

As a complement to the analyses of the after-contraction phenomenon, arm abduction movements induced by unilateral deltoid muscle vibration were studied in all fourteen subjects. The vibrator was applied with a small, cylindrically shaped DC motor (3·5 cm × 7 cm; weight, 140 g) with an eccentrically loaded axis. The amplitude and frequency of vibration was 1 mm and 100 Hz, respectively. The standard procedure was as follows. With the blindfolded subject standing with the arm in a slightly abducted position (requiring a weak background abductor contraction) the vibrator was manually applied over the deltoid muscle. During the vibration period, which lasted 10–20 s, attempts were made to maintain a constant force of application. The instructions to the subject were the same as in the after-contraction trials, i.e. not to actively interfere with any arm movements that might be perceived as non-volitional.

RESULTS

Effects of varying individual steps in the conditioning procedure

Figure 1*A* shows goniometer recordings from a trial in which a control type of conditioning procedure was carried out bilaterally, i.e. also in the 'test' arm for which the procedure was modified in the other four types of trials. In this example the non-volitional arm abductions started about 3 s after completion of the arm return movements and reached their peak amplitude within 12–16 s. The corresponding mean values for the ten subjects were 2·9 s (range, 1–7 s) and 17·6 s (range, 9–32 s), respectively. In Fig. 1*A* the after-contraction movement was somewhat smaller for the test arm, but as illustrated by Fig. 2 (trial A) the mean values for the test and control arm were about 8 deg and showed, as expected, no significant difference.

As shown in Fig. 2 (trials B–E), all four types of deviations from the control type of conditioning procedure (see Methods and figure legend) resulted in a significantly ($P < 0.01$) smaller abduction movement in the test arm than in the corresponding control arm. In fact, such an asymmetry was without exception observed in all ten subjects for all four types of trials. An example of such an asymmetric after-contraction phenomenon is illustrated in Fig. 1*B*. In this case the non-volitional abduction was missing in the test arm. In this and some other individual trials the test arm instead exhibited a small adduction (expressed as a negative value).

Effects of changes in intramuscular temperature

In the trials where, prior to a bilateral control type of conditioning procedure, the test arm shoulder region had been warmed (Fig. 3) the non-volitional arm abductions were significantly lower in the test than in the control arm ($P < 0{\cdot}05$). After shoulder cooling the test arm values were instead higher than the control arm values (Fig. 3), but this difference was non-significant ($P = 0{\cdot}15$).

Additional observations

The following observations, which are in agreement with earlier literature reports, were made without any attempt to collect data sufficient for statistical evaluation.

Facilitatory influence of background contraction. According to Hick (1953) instructions to relax have an attenuating effect on the after-contraction phenomenon. For that reason, the subjects participating in the bilateral trials described above were instructed not to relax but to hold the arms immediately after the conditioning procedure in the same, slightly abducted position that they were in before the procedure. In a series of unilateral trials which included deltoid EMG recordings results were obtained which fully agree with those reported by Hick. As exemplified by Fig. 4, the after-contractions were weaker and had a longer onset latency when there was no background contraction. Similar

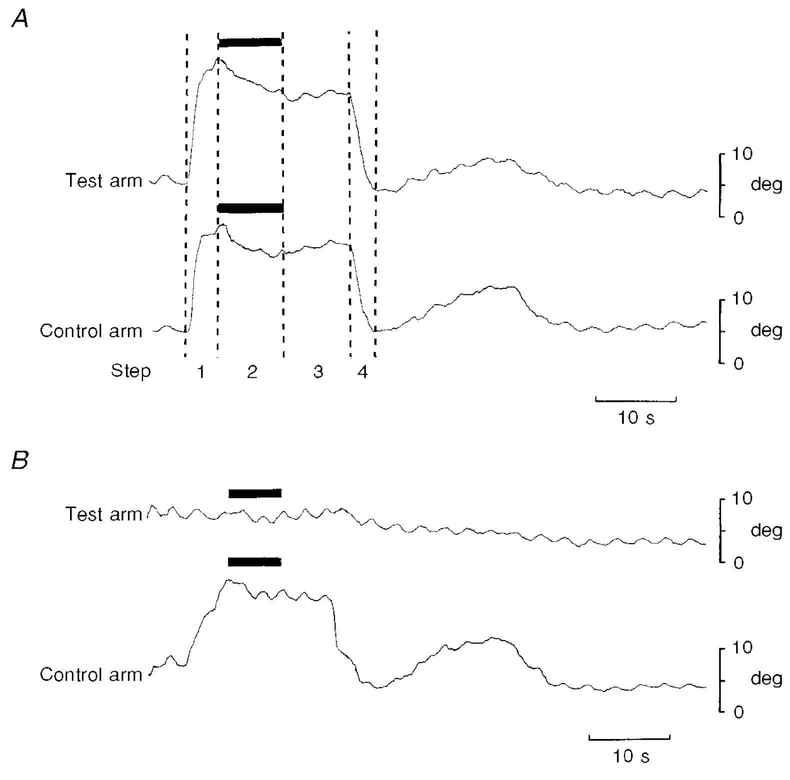


Figure 1. Examples of postural after-contraction movements

A, goniometer traces showing non-volitional arm abduction movements in the right (Test) and the left (Control) arm following a bilateral 'control type of conditioning procedure' consisting of four steps: active arm abduction up against the stands (step 1), forceful abductor contraction for 5–10 s against the stands (step 2; indicated also by filled bar), relaxation during 4–8 s while the experimenter held the arms against the stands (step 3), and lowering of the arms back to the initial slightly abducted position during 3–5 s; this was performed by the experimenter during continued relaxation (step 4). *B*, non-volitional abduction movement missing in test arm for which the conditioning forceful abductor contraction (indicated by filled bar) was performed in the initial intermediate position of the arm (i.e. where the abductor 'hold-short' requirement was not fulfilled). Arm abductions are indicated by upward deflections in goniometer traces. In this and in Figs 4–6 the calibration mark 0 deg indicates the natural resting position of the arm during relaxation. Low-amplitude oscillations in goniometer traces were induced by respiratory chest movements.

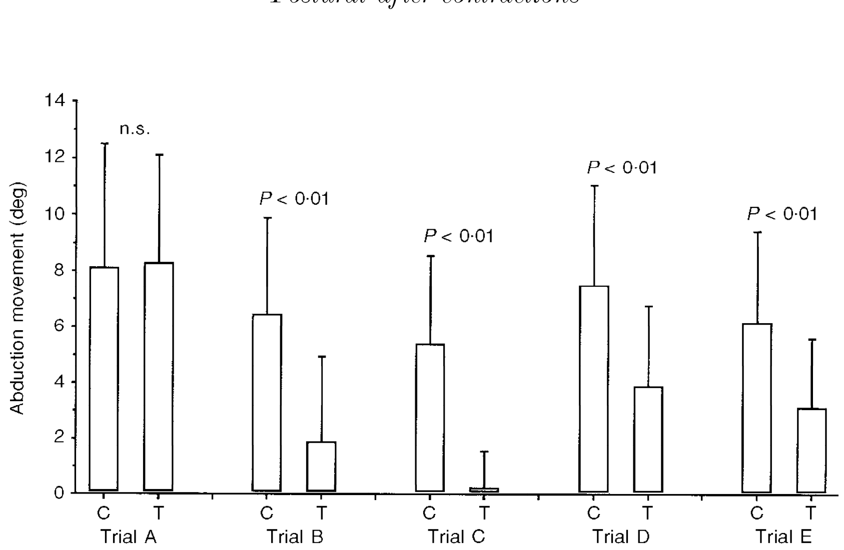


Figure 2. Effects of changes in conditioning procedure on postural after-contraction movements

One of the arms was always exposed to a 'control type of conditioning procedure' while the test arm was exposed either to the same type of procedure (trial A) or to a procedure which in one of the following specific ways differed from that in the control arm: omission of initial arm abduction movement (trial B), omission of forceful 'hold-short' abductor contraction (trial C), omission of post-contraction 'hold-short' relaxation period (trial D), and fast instead of slow return movement to intermediate position (trial E). For each type of trial, paired columns indicate mean ± S.D. ($n = 10$) of the ensuing non-volitional arm abductions in the control (C) and the test (T) arm, and the level of significance for the asymmetry is indicated.

results were obtained in all six subjects exposed to this kind of test.

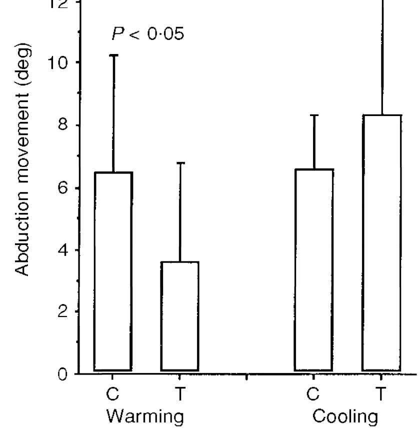
Signs of extrafusal thixotropy. As can be seen in Fig. 4*A*, the deltoid EMG activity was lower immediately after than before the conditioning manoeuvre even though the arm on the two occasions was held in a similar slightly abducted position. Such post-manoeuvre reduction in the background abductor EMG activity was also clearly seen in the four 'non-responders' who after the control type of conditioning procedure exhibited no apparent signs of postural after-contractions (example shown in Fig. 5). As pointed out in earlier studies where similar observations were made (Hagbarth, Nordin & Bongiovanni, 1995; Nordin & Hagbarth, 1996) a probable explanation is that the voluntary effort and skeletomotor output required to hold a limb in a given anti-gravity position is lower after a conditioning procedure which enhances the inherent stiffness of the extrafusal muscle fibres.

Similarities between postural after-contractions and tonic vibration reflexes

In individual subjects there was an obvious similarity in the velocity of the non-volitional arm abductions induced by preceding 'hold-short' conditioning procedures and those induced by deltoid muscle vibration. A typical example is shown in Fig. 6.

Figure 3. Effects of changes in intramuscular temperature on after-contraction movements

In both arms a 'control type of conditioning procedure' was performed. Prior to this the shoulder region of the test arm was either cooled or warmed. For each type of trial paired columns indicate mean ± S.D. ($n = 10$) of the ensuing non-volitional arm abductions in the control (C) and the test (T) arm, and the level of significance for the asymmetry is indicated.



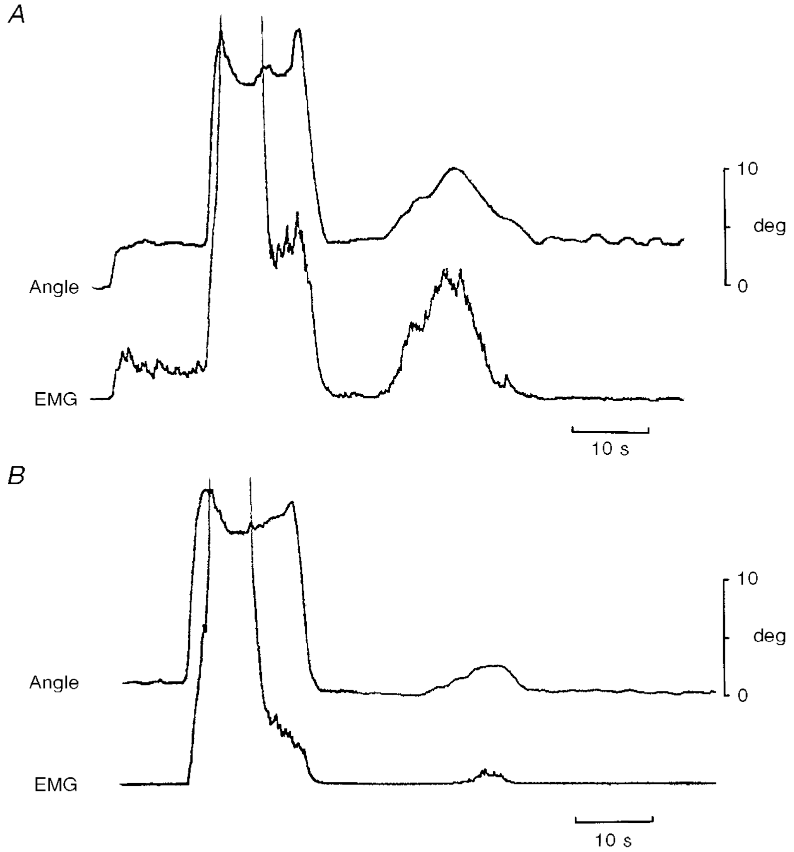


Figure 4. Effects of voluntary background contraction on postural after-contractions

Arm abductor postural after-contractions provoked by a 'control type of conditioning procedure with (*A*) and without (*B*) voluntary background abductor contraction. Note shorter latency and higher amplitude of after-contraction movement in *A*. Note also in *A* the higher level of abductor mean voltage EMG activity before than immediately after the conditioning procedure, even though the subject on both occasions held the arm in the same, slightly abducted position.

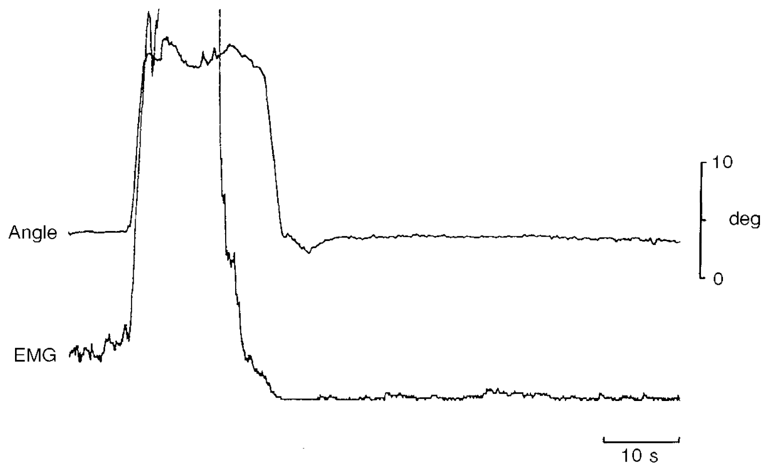


Figure 5. After-effect of conditioning procedure on background EMG activity

Example from one of the 'non-responders' who exhibited no obvious arm abductor postural after-contractions following the 'control type of conditioning procedure'. The only apparent after-effect of the procedure is a reduction in the level of abductor mean voltage EMG activity required to hold the arm in the slightly abducted position of about 3 deg.

As judged by the reports of the subject in whom both postural after-contractions and tonic vibration reflexes could be evoked in the arm abductor muscles, the two types of non-volitional muscle contractions were accompanied by similar lightness illusions; in both cases it was felt as if the arm was lifted by some outer force.

As has previously been reported (Eklund & Hagbarth, 1966) tonic vibration reflexes are facilitated by a weak voluntary background contraction in the muscles exposed to vibration. The observation that such voluntary background contractions also have a facilitatory influence on postural after-contractions (see above) provides another example of similarity.

It is well known that these two motor phenomena vary in strength from one subject to the next. However, so far no attempts have been made to determine whether they vary independently of each other or exhibit interindividual co-variance. An indication of such co-variance was obtained in the present study in which it was found that the four subjects classified as 'non-responders' to the control type of conditioning procedure also differed from all the others in that no detectable arm abductions occurred in response to deltoid muscle vibration.

DISCUSSION

The muscle spindle thixotropy hypothesis

The present results provide evidence that muscle spindle thixotropy plays an important role in the genesis of postural after-contractions. The evidence is based on the following observations. (1) The most pronounced after-contraction movements were evoked by that particular type of hold-short conditioning procedure which in various respects mimicked the procedure that according to animal experiments is especially effective in provoking thixotropic excitation of primary spindle endings (Fig. 2). (2) Changes in intramuscular temperature affected the strength of the after-contraction phenomenon in a direction predicted by the thixotropy hypothesis (Fig. 3). (3) Given that extra- and intrafusal muscle fibres possess similar thixotropic properties, the signs of increased extrafusal stiffness after hold-short conditioning procedures (Figs 4*A* and 5) can be regarded as an indication that a parallel stiffness change occurred in the intrafusal fibres.

A finding of particular relevance is that conditioning arm abductor contractions that did not fulfil the 'hold-short' requirement were comparatively ineffective in producing after-contraction movements (Fig. 2, trial B). This finding, which is fully consistent with the thixotropy hypothesis, is hard to reconcile with the proposal of Granit (1972) that postural after-contractions largely depend on 'post-tetanic potentation' of α-motoneurones following the spindle activation during the voluntary effort preceding the after-effect. Nevertheless, the present results do not rule out the possibility that excitability changes in central reflex paths may contribute to the development of after-contractions. Possibly, such central effects are responsible for the comparatively weak after-contractions which could also be evoked in some subjects when the conditioning voluntary contraction was performed without a preceding arm elevation. It is of interest to note that the after-contractions in the human elbow flexor and extensor muscles which Gilhodes *et al.* (1992) attributed to central excitability changes were evoked by conditioning contractions which did not fulfil the 'hold-short' requirement, i.e. contractions similar to our trial B test arm contractions.

So far, no human microneurography studies have been made to explore whether, as expected, the 'hold-short' type of conditioning procedure used in the control trials of the present study is particularly effective in producing a post-contraction enhancement in afferent spindle discharge. For human finger flexor muscles it has been shown, however, that, compared with isometric voluntary contractions at a given intermediate muscle length, conditioning shortening contractions are more effective in inducing post-contraction enhancement in muscle stiffness and in muscle afferent resting discharge (Hagbarth, Hägglund, Nordin & Wallin, 1985; see also Hutton *et al.* 1987; Jahnke, Proske & Struppler, 1989). In conformity with the findings of Hagbarth *et al.* (1985), Ribot-Ciscar, Tardy-Gervet, Vedel & Roll (1991) found no overall enhancement in the discharge rates of muscle spindle afferents following strong voluntary isometric contractions at a given intermediate muscle length. By contrast, Wilson, Gandevia & Burke (1995), who

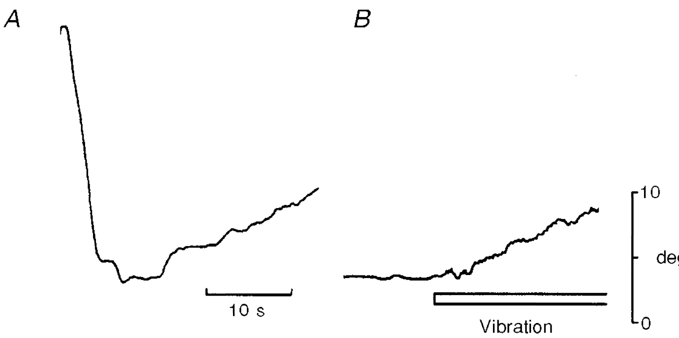


Figure 6. Similar time course of after-contraction movement and movement induced by muscle vibration

Example from one subject showing similarity in the velocity of non-volitional arm abduction movements induced by a 'control type of conditioning procedure' (*A*) and by vibration applied over the deltoid muscle (*B*). In *A*, the initial downward deflection in the goniometer trace illustrates the passive arm return movement following the conditioning 'hold-short' abductor contraction.

also searched for after-effects of isometric voluntary contractions on afferent spindle discharge, found that for a population of fifty-five spindle afferents the mean post-contraction discharge rate was 65% higher than the mean pre-contraction discharge rate. The divergent results are not totally unexpected. As pointed out by several investigators (Jahnke *et al.* 1989; Proske *et al.* 1993; Nordin & Hagbarth, 1996) the after-effects of a conditioning isometric voluntary contraction are highly dependent on the unconditioned state of the muscle, in which the stiffness or slackness of both extra- and intrafusal muscle fibres at any given time may vary as a result of thixotropic after-effects which remain after preceding movements and/or contractions.

It has previously been demonstrated that antagonistic muscles are co-activated during forceful voluntary isometric contractions of a given muscle group (Psek & Cafarelli, 1993). Thus, it is probable that in the present experiments the forceful hold-short arm abductor contractions were also accompanied by contractions in the arm adductors for which the conditioning contractions were of the 'hold-long' type. In compliance with the hypothesis of Proske *et al.* (1993) and the reasoning of Wise, Gregory & Proske (1996) one would then expect that after return to the test position the spindles in the adductor muscles were slack so that, in contrast to the enhancement of the arm abductor spindle discharge, the adductor spindle discharge was reduced.

It is an old observation that a postural after-contraction evoked in one of the arms can facilitate or even produce an after-contraction in the other (for references, see Granit, 1972). Such a facilitatory interaction between responses in the two arms might explain why, in the series of paired comparisons illustrated in Fig. 2, the control arm response tended to be lower the more the test arm response was reduced by the deviation from the control procedure. It is also conceivable that without such a crossed facilitatory influence the test arm responses would have been lower than indicated.

Other examples of reflex consequences of muscle spindle thixotropy

Not only the resting discharge of primary spindle afferents but also their sensitivity to muscle stretch and vibration are dependent on the previous history of movements and contractions. Both animal experiments and human studies indicate that as a consequence of muscle spindle thixotropy the stretch and vibration sensitivity of primary spindle endings is enhanced following 'hold-short' conditioning procedures, and that such spindle sensitization in turn results in an enhancement of both short-latency phasic stretch reflexes and tonic reflex responses to muscle vibration (besides review of Proske *et al.* 1993, see Hagbarth *et al.* 1995; Nordin & Hagbarth, 1996). As judged by the present results, the postural after-contraction phenomenon represents a further example of a reflex consequence of muscle spindle thixotropy.

Comparisons with effects of muscle vibration

With the interpretation of the after-contraction phenomenon given above it was not surprising to find several similarities between this phenomenon and the tonic vibration reflex. Our proposal is that, independently of whether an increase in the level of afferent spindle discharge is induced by vibration or by a preceding hold-short conditioning procedure, the α-motoneurones of the muscles concerned are via the stretch reflex arc exposed to a rise in autogenetic excitatory inflow. When this excitatory influence by temporal summation becomes strong enough it leads to a non-volitional rise in skeletomotor outflow. The fact that both vibration reflexes and postural after-contractions are facilitated by a voluntary background contraction can be regarded as an expression of the 'automatic gain compensation' principle (Matthews, 1986).

The lightness illusions which accompany both tonic vibration reflexes and postural after-contractions can, at least in part, be attributed to the fact that with a rise in spindle-mediated reflex support to the skeletomotor outflow less activation of cortical motor centres is required to maintain a desired muscle force. Lightness illusions due to such relief of cortical motor centres may also result from enhanced extrafusal stiffness following hold-short conditioning procedures (Figs 4*A* and 5). It is an old observation that lifting a weight a few times leaves an after-effect making a subsequently lifted, lighter weight feel lighter than before (Müller & Schuman, 1889). Since weight-lifting involves a component of hold-short voluntary contractions, such lifts may well leave an after-effect of increased intra- and extrafusal stiffness, both of which may contribute to the lightness illusions. More recently Hutton *et al.* (1987) showed that blindfolded subjects trained to make a series of weak elbow flexor contractions of equivalent predetermined strength constantly made errors in the direction of a positive bias when, after a more forceful elbow flexor contraction, they tried to reproduce the desired low force contractions.

Not only weight or power illusions, but also distortions in position sense have been documented in connection with tonic vibration reflexes and as after-effects following hold-short and hold-long conditioning procedures. In particular, it has been shown that following a hold-short contraction of the biceps muscle the subject perceives the arm to be more extended than it really is (Gregory *et al.* 1988), i.e. an illusion similar to that which can be induced by vibration of the arm flexor muscles (Goodwin, McCloskey & Matthews, 1972). These findings support the proposal that the muscle spindles by their cortical projections contribute to the sense of position.

Functional implications

A relevant question is to what extent postural after-contractions with accompanying weight and positional illusions can affect motor performance in skilled motor acts. It is to be expected that distortions in weight perception and position sense will have negative effects on motor control in situations where great precision is required. There may well be a causal relationship between the temperature dependency of the after-contraction phenomenon (Fig. 3) and the beneficial effects of warming-up exercises carried out by athletes.

Still, the possibility remains that thixotropy-dependent motor and perceptual after-effects may have a positive influence on certain types of motor activities. As previously pointed out by Sapirstein *et al.* (1937) and Hutton *et al.* (1987) it cannot be excluded that under certain conditions the after-effects may serve as a driving force behind certain types of rhythmical alternating movements, such as those involved in walking, breathing and chewing. Provided that such movements involve components of hold-short contractions against a restraint and are not too fast, each cycle may lead to a thixotropy-induced spindle excitation which promotes the initiation of the next cycle.

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