RAPID REPORT

Motor commands contribute to human position sense

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The role of afferent inflow and efferent outflow (or command) signals in judgements of limb position has been debated for over a century. One way to assess this is to check for changes during complete paralysis, with the current view being that perceived movements or position changes do not usually accompany attempts to contract paralysed muscles. To re-examine this, we asked six naïve subjects to carry out a simple position-matching task at the wrist. In the absence of vision, subjects accurately perceived the position to which their right wrist had been moved by the experimenter by matching it with their left hand. There was no significant change in perception when position was matched during sustained flexion or extension efforts. Then we paralysed and anaesthetized the right arm with ischaemia in order to produce a 'phantom' hand. The perceived position of the wrist changed by more than 20 deg when subjects attempted to flex or extend their hand when it was paralysed and anaesthetized. Further studies showed that this illusion was not dependent on the way in which the paralysis was produced and that the size of the position illusion increased when the level of effort during paralysis increased. These results establish for the first time a definitive role for 'outflow' signals in position sense.

The role of afferent ('inflow') and efferent ('outflow') signals in proprioceptive and visual judgements has long remained the subject of controversy. The debate has focused particularly on judgements of the position of objects in space and on two components of proprioceptive sensation: that involved with perceived limb movement and position, and that involved in judgements of force and heaviness (McCloskey *et al.* 1983). While a role for efferent signals cannot be ruled out in distinguishing between self-generated events and events generated by an external agency (Frith *et al.* 2000), the precise operation of these systems remains unresolved and difficult to reveal experimentally.

In vision, since von Helmholtz (1867) it has been argued that the perceived position of an object in our visual world depends on knowing where it is on the retina and on the position of the eye. Eyeball position can be signalled either by ocular proprioceptors or by a 'sensation of innervation'. This sensation of innervation, or outflow signal, is also termed a corollary discharge in the terminology introduced by Sperry (1950) or efference copy in the terminology introduced by von Holst (1954). These two terminologies have been used extensively although their original introduction was intended to

explain motor behaviour rather than perceptual events. Currently, both afferent signals from ocular muscles and centrally generated signals of innervation are thought to contribute in varying degrees to perceived eyeball position (Donaldson, 2000).

In proprioception involving limb muscles, judgements of force and of heaviness of lifted weights have been shown to depend not only on afferent signals about force but also on signals of central origin associated with the level of perceived force. Such sensations are usually termed signals of central motor command or effort. The involvement of motor command signals in force sensation explains why the apparent heaviness of objects lifted by weakened muscles increases under a variety of clinical (e.g. Holmes, 1917; Gandevia & McCloskey, 1977) and experimental circumstances (e.g. McCloskey *et al.* 1974; Gandevia & McCloskey, 1977; Weerakkody *et al.* 2003). An illusion of increased force or heaviness occurs when signals related to an increased central command or effort are required to generate the same force (for review see Gandevia, 1987).

Here we raise the question of whether a signal of central origin can contribute to limb position sense. Most of the available evidence favours inflow from muscle as providing the major position signal (for reviews see McCloskey, 1978;

Matthews, 1982). However, it is becoming increasingly clear that receptors in the skin also contribute at many joints (Edin & Johansson, 1995; Collins & Prochazka, 1996; Collins *et al.* 2005). Whether there is an additional signal of central origin remains the subject of controversy. There are inconsistent reports of perceived movements and changes in position during willed movements of limbs paralysed by disease, in experimental paralysis (McCloskey & Torda, 1975; Gandevia *et al.* 1993*a*), or during willed movements of phantom limbs, following amputation or deafferentation (Ramachandran & Hirstein, 1998; Frith *et al.* 2000). The most direct test in healthy subjects was that by McCloskey & Torda (1975) who examined whether attempted movements of muscles paralysed with a local infusion of tubocurarine produced sensations of movement. Attempted contraction of the acutely paralysed muscles did not apparently result in an illusion that they had moved or been displaced. This result supported earlier observations (Goodwin *et al.* 1972), and the issue seemed settled.

Recent studies of position matching at the elbow have revealed that a systematic matching error emerges when elbow flexors are fatigued (Walsh *et al.* 2004; Winter *et al.* 2005; Allen & Proske, 2005). These results have been interpreted as evidence in favour of an effort-based signal contributing to position sense during limb placement in the presence of the force of gravity. However, these results do not distinguish between use of such a signal as an indicator of force or of position.

Therefore, the present study was designed to re-investigate this issue. We used paralysis and anaesthesia to remove any movement-related feedback from the arm and hand and to generate a phantom sensation of the 'dead' hand. Our results reveal the existence of large illusions of limb position, attributable to a sensation of innervation.

Methods

Studies were performed on eight adult subjects. The main experiment was conducted on six subjects who were unaware of the hypotheses under test. Pilot studies had earlier been conducted on two authors (SG, JT) with similar results to those reported in the main study. These two subjects were re-studied after the main experiment to extend one aspect of the findings (see Results). Informed consent was obtained. The procedures were approved by the local institutional ethics committee and the study conducted according to the Declaration of Helsinki.

General procedures

Subjects were comfortably seated with the right forearm strapped to a table and the hand held in a manipulandum that rotated in the flexion–extension plane about the wrist.

The fingers were clamped in full extension. The wrist could be moved to different angular positions and fixed in place so that any contractions of wrist muscles were isometric. Wrist angle was deemed to be at 0 deg with the metacarpal in line with the forearm, with negative angles in the direction of flexion and positive angles in extension. Maximal voluntary torque was measured for flexion and extension efforts at 0 deg before the start of the position matching. During the main part of the study, the right forearm, hand and apparatus were covered so that they could not be seen by the subject.

Small areas (∼10 mm diameter) were marked at three sites: one on one of the digits, a second just proximal to the wrist, and a third just distal to the elbow. These sites were used for sensory testing during development of ischaemic paralysis and anaesthesia (see below). Surface electromyographic activity (EMG) was recorded with electrodes over flexor carpi radialis and extensor carpi radialis (interelectrode distance ∼50 mm). The perceived position of the right wrist was signalled using a large protractor marked in degrees and mounted coaxially above the wrist turntable. Subjects used the left hand to turn the arm of the goniometer to match the perceived wrist position, but were unable to see the marked angles.

A wide cuff with two chambers was positioned on the upper arm and connected to a regulated pressure source so that the cuffs could be simultaneously inflated to 300 mmHg in less than 1 s. This arrangement produced more consistent blocks than achieved with a conventional sphygmomanometer cuff inflated more gradually. Sensory tests included assessments of tactile sensation with von Frey hairs and a cotton swab. Temperature sensation was tested with warm and cold metal rods applied to the skin surface. Pain perception was assessed by firm pinching of the skin. These tests were carried out before inflation of the cuff and at intervals of 5–10 min after inflation. Usually by 40 min after inflation, light touch was abolished with the only residual sensation being a burning sensation produced by painful pinching of the skin just below the elbow. At this stage, voluntary movement was abolished for wrist and finger movements. This was formally checked using electromyography (Fig. 1).

Experimental protocol

After a brief familiarization, control measurements were performed. The right wrist was passively moved randomly into flexion or extension and then fixed at one of six positions (−30, −20, −10, 0, +10 and +20 deg). To minimize any effects due to muscle thixotropy the wrist was moved back and forth manually through 30 to 90 deg several times before the final position was reached. The subjects were then asked to move the pointer to match the perceived position of the wrist. Each position was matched

three times: once at rest, once with a flexion effort of about 30% maximum, and once with an extension effort of 30% maximum. For the first set of matches the subject had visual feedback of the required flexion and extension torques. For the second set the subject had to reproduce these efforts from memory without visual feedback of torque. Previous studies had established that subjects can grade their motor output to muscles during paralysis (e.g. Gandevia *et al.* 1993*a,b*). Subjects were asked to exert the required torque, to maintain it for 1–2 s and then to 'match the position of the right wrist', while their effort continued. The subject then relaxed and further trials were conducted.

The final set of matches began when wrist and hand muscles were completely paralysed and virtually all sensation was abolished below the cuff. Subjects had been asked to refrain from movements during development of the block. This was done to minimize discomfort but it also meant that subjects were unaware that the final set of matches were performed with no EMG activity or movement accompanying their voluntary efforts. Although undetected by the subject, the position of the right wrist was varied, just as before the block.

In the two additional experiments similar procedures were followed with three changes. First, prior to cuff inflation, an intravenous line had been placed on the dorsum of the right wrist. After cuff inflation, a large bolus injection of lignocaine (200 mg in 40 ml of saline) was delivered to shorten the time to full paralysis and to ensure that all sensation was lost below the cuffs including sensations initiated by small-diameter afferents. Second, two levels of voluntary efforts were used (20% and 50% maximum). Again, the angular position, direction and level of effort were randomised, with two trials each. Third, three angular positions were used: −20, 0 and +20 deg.

Recording and analysis

Angular position and torque at the wrist were recorded together with the EMG of wrist muscles (Cambridge Electronic Design, 1401 interface). Subjects were asked to describe any sensory changes in the right arm during development of the block after each set of sensory tests and before the third set of position matching. They were asked to comment on the position of their fingers, wrist and forearm and then their elbow. Comments
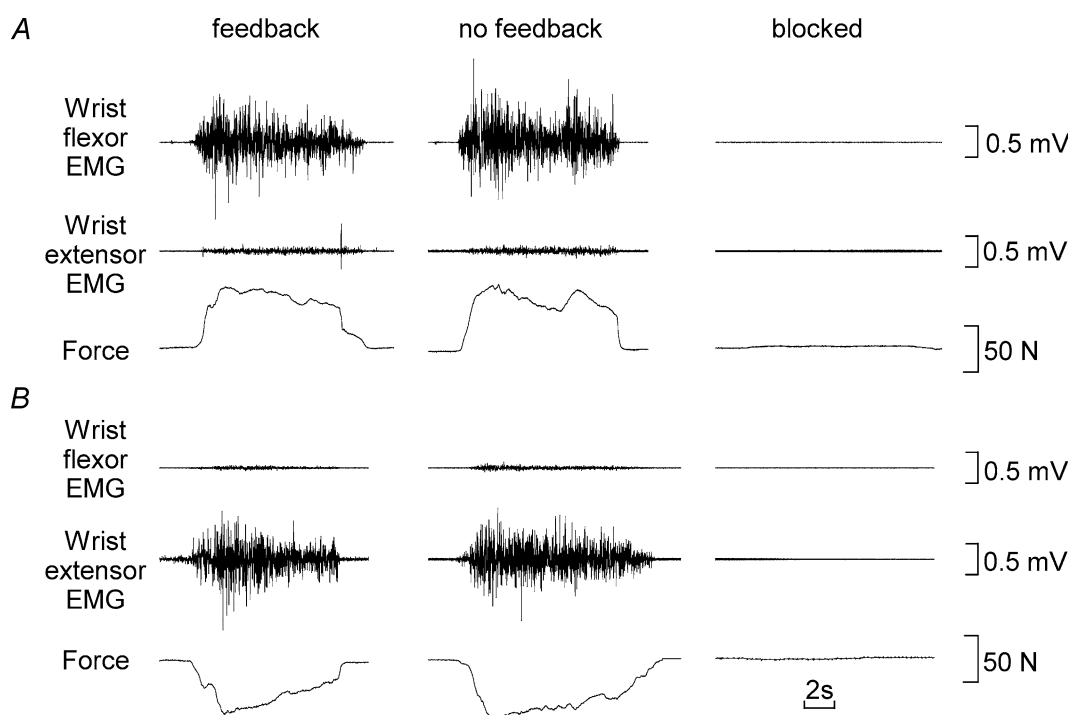
Figure 1. Typical recordings during which a subject signalled perceived position of the wrist
Typical single trials from one subject to show EMG from the wrist flexors and extensors, and force, during flexion and extension efforts with force feedback (set 1, 'feedback'), without force feedback (set 2, 'no feedback'), and when paralysed and anaesthetized (set 3, 'blocked'). Force and EMG were similar with and without feedback, while no EMG or force was produced during attempted efforts when paralysed. During recordings, an experimenter marked the onset of efforts and these marks were used to determine the onset of efforts when no EMG or force occurred.

were taped and transcribed. Subjects described the sensory experience during the matching experiments when sensation and movement had recovered (about 10 min following deflation of the cuff). The dependence of perceived position on actual wrist position both before and after paralysis was also checked using regression analyses. The main analysis focused on whether the perceived position of the right wrist was altered when subjects exerted a flexion or extension effort under control conditions and during paralysis. Regression analysis of perceived wrist position against actual wrist position was performed. If subjects matched perfectly, the regression line for actual and perceived wrist position would have a gradient of 1.0 and an intercept of 0 deg. Additionally, there would be no difference between regression lines for judgements at rest and when flexion and extension efforts were made. Statistical significance was set at the 0.05 level.

Results

Subjects carried out position-matching trials with and without flexion or extension efforts involving muscles at the right wrist by indicating the position with their left hand. Wrist position sense was measured before and after ischaemic paralysis and anaesthesia produced by a blood pressure cuff inflated above arterial pressure. Figure 1 shows typical EMG and force traces for flexion and extension efforts during the two sets of control trials. In the first set, subjects had feedback of force at the wrist, but this was withdrawn in the second set, prior to cuff inflation. Subjects were able to produce consistent force

and EMG levels from memory in the second set when visual feedback of force was not available. This procedure allowed subjects to make reasonable attempts at generating given efforts during paralysis.

Before paralysis, subjects accurately detected the position of the wrist when the hand had been passively moved into flexion or extension, across the angular range. Figure 2 shows data from a typical subject. Trials in which an effort was generated with or without visual feedback have been combined and averaged. For passive matching, values lie close to the line of proportionality, that is, the different positions were accurately perceived. Small, insignificant errors were present when subjects exerted efforts in one direction or the other. Linear regressions of perceived and actual wrist angle across subjects showed consistent trends: When subjects performed matching at rest, the gradient of the regression line was about 1 and intercepts of the regressions were close to 0 deg (rest −0.3 deg; flexion 2.5 deg; extension 4.3 deg). The mean change from the angular error during the isometric contraction compared with the passively matched position was 2.4 ± 4.4 deg (mean $\pm$ s.d.) in the direction of flexion with flexion contractions and 5.4 ± 7.0 deg in the direction of extension with extension contractions, but these effects were not statistically significant ($F < 3.5$, $P > 0.118$).

With the hand positioned at 0 deg, after ~40 min of ischaemia, all voluntary movements were blocked, as confirmed by electromyography (Fig. 1), and all sensations, apart from pain in response to a skin pinch, were abolished from just below the elbow. By this stage, all subjects had reported the presence of a phantom hand in
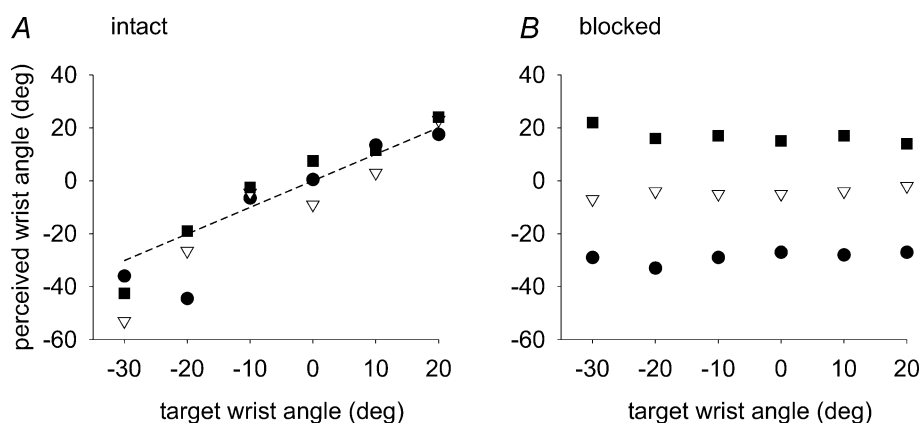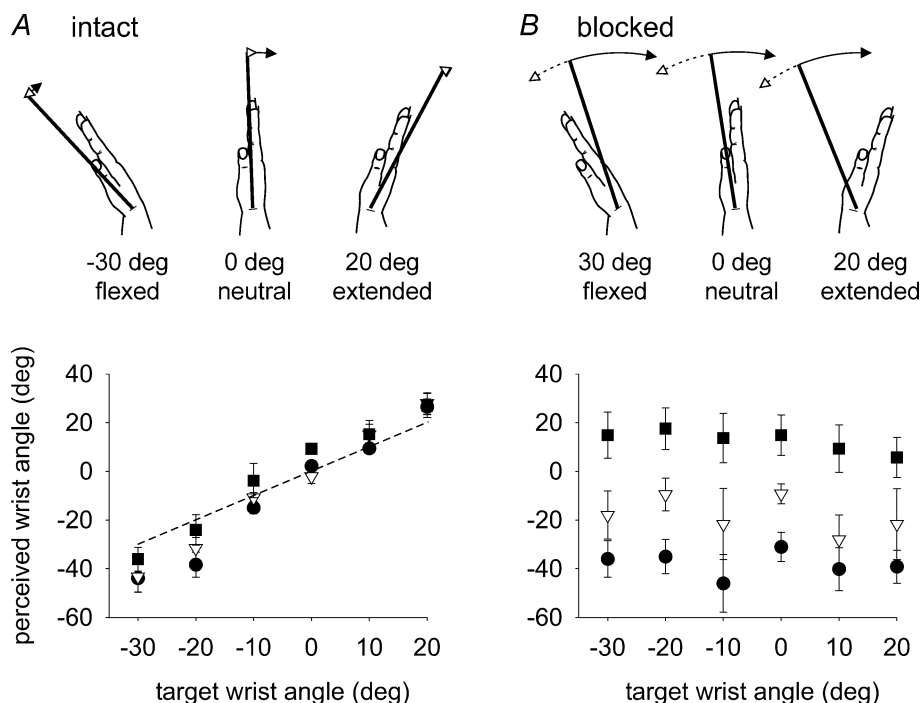

Figure 2. Flexion and extension efforts change the perceived position of a phantom hand in a single subject
A, the perceived angle at the wrist without additional effort (∇), with flexion efforts (●), and with extension efforts (■) plotted against test angles from −30 deg to +20 deg before paralysis and anaesthesia ('intact'). A dotted line indicates the line of identity. In this and subsequent figures negative values indicate flexion and positive ones extension. *B*, the same display as in *A* but after the hand had been paralysed and anaesthetized ('blocked'). The neutral position of the phantom hand is slightly flexed (∇). Attempted flexion or extension movements at 30% maximum effort caused large additional displacements (independent of the starting positions) in the direction of flexion for flexion efforts and in the direction of extension for extension efforts.

which the fully extended fingers were perceived as flexed at all joints, as in a grasp. Three subjects also reported that the wrist felt flexed while anaesthesia developed, despite being fixed at 0 deg. This observation supports the slightly flexed position that subjects selected when the hand was placed at 0 deg (9.3 ± 10.0 deg; one-sample $t = 2.3$, $P = 0.072$; see also Figs 2*B* and 3*B*). However, a similar wrist position was signalled across all actual test positions (mean 18.0 ± 25.5 deg into flexion). Thus, the linear relationship between actual and perceived position observed before paralysis was now lost. Regressions of perceived and actual angle across subjects showed that gradients were now close to 0 and the intercept was 18.9 deg into flexion. When subjects were asked to make flexion efforts, all values were in the direction of flexion (mean 38.1 deg). Similarly, for extension efforts, values were in the direction of extension (mean 11.7 deg). Hence, when subjects attempted a flexion or extension effort with the phantom hand, consistent displacements of the perceived position were observed, independent of its actual position.

In debriefing after recovery of sensation and movement, two subjects reported that the phantom hand had moved slowly in response to the applied effort ('as if moving through treacle'), while one reported that the hand was in the altered position without an accompanying illusion of motion. Two subjects also reported that the hand moved back to the neutral position when they ceased making an effort. One reported that 'it slowly returned back to its original neutral position' and the other that it 'bounced back to the middle'. Additionally, one subject reported that the perceived position of the paralysed hand depended on the level of effort: 'The amount of effort that you put in to move the arm when it's paralysed appears to resemble the amount of movement that you get. So, the more effort you put in, the more movement you get out of it.' This point was specifically assessed in the second set of experiments.

In these two studies, a lignocaine injection was used to hasten the onset of effects of ischaemia. In addition, this ensured that all fusimotor axons and small-diameter afferents were blocked below the cuff. Two levels of effort were used (20% and 50% of maximum). During paralysis,

Figure 3. Group data for the change in perceived position of a phantom hand during flexion and extension efforts
A, upper panel, positions of the hand during matching, with angles at the wrist given in degrees. When the hand was placed at each angular position, its position as perceived by the subject is indicated by the continuous line. Arrows at the end of the line indicate the size of any additional displacements perceived when subjects attempted to flex (open arrow) or extend (filled arrow) their hand from that position. The length of the arrows indicates the size of the perceived displacement produced by attempted movement. Lower panel, the perceived angle at the wrist (mean ± s.e.m.) without additional effort (∇) with flexion efforts (●) and with extension efforts (■) plotted against test angle. *B*, the same displays as in *A* but after the hand had been paralysed and anaesthetized. The neutral position of the phantom hand is slightly flexed. Attempted flexion or extension movements at 30% maximum effort caused perceived displacements in the direction of the applied efforts.

the same result was observed, with a perceived change in the position of the wrist during voluntary effort (Fig. 4).

As with the first experiments, before paralysis the gradient of the regression lines was close to 1.0 for judgements at rest and for both levels of effort, with intercepts close to 0 (not shown). However, when the hand was paralysed, the gradients of the regression lines were about 0, while the intercepts depended on the level of effort. At rest, the average intercept was −2.5 deg. With low flexion efforts it was 28.7 deg in the direction of flexion and with high flexion efforts 47.5 deg into flexion. With extension efforts the intercepts were 26.2 deg and 44.3 deg in the direction of extension with low and high efforts, respectively. Thus, when the subject was paralysed, subjects perceived large shifts in wrist position when efforts were made, independent of actual wrist position and these shifts increased with greater effort.

Discussion

This study provides direct evidence that signals related to the motor command or effort can produce an illusion that a part of the body has been displaced even though it has not moved. In all subjects deafferentation produced by the ischaemic block led to the perception of a phantom hand. The generation of a phantom hand in normal subjects with anaesthetic block of sensory and motor nerves of the arm has been reported previously (Melzack & Bromage, 1973). In this phantom, under relaxed conditions, the fingers and thumb were flexed and the wrist was also slightly flexed. By forcing subjects to indicate the wrist position of their

phantom we have uncovered a large position signal driven by signals related to motor commands.

The deafferentation and paralysis were generated using an ischaemic block with a sphygmomanometer cuff on the upper arm. This produced complete paralysis as checked by loss of voluntary movement of the wrist and hand and EMG silence, and loss of all sensation mediated by large sensory fibres below the elbow. This would have eliminated all inputs from cutaneous, joint and muscle receptors. However, while pain sensation was lost distally, a little remained around the elbow. Although it was unlikely that this could have generated any signal of wrist position, we confirmed the existence of an illusion of joint displacement in two subjects in whom paralysis and deafferentation were produced by intravenous lignocaine infusion below the cuff. This method of anaesthesia ensured a total nerve block including all small-diameter fibres. In these subjects the illusion of displacement increased with increased levels of effort. Thus, we conclude that the displacement illusion did not require any sensory signal for its generation and that it could be graded with the level of motor command. Gradation of the size of the illusion with effort may mean that signals of motor command are more important for position sense during loaded rather than unloaded contractions.

On theoretical grounds, it has long been recognized that judgements of position require a mechanism to separate position changes produced by an external agency and those that are self-generated (Matthews, 1988). However, the usual explanation has been that signals of motor command contribute to sensations of force and heaviness
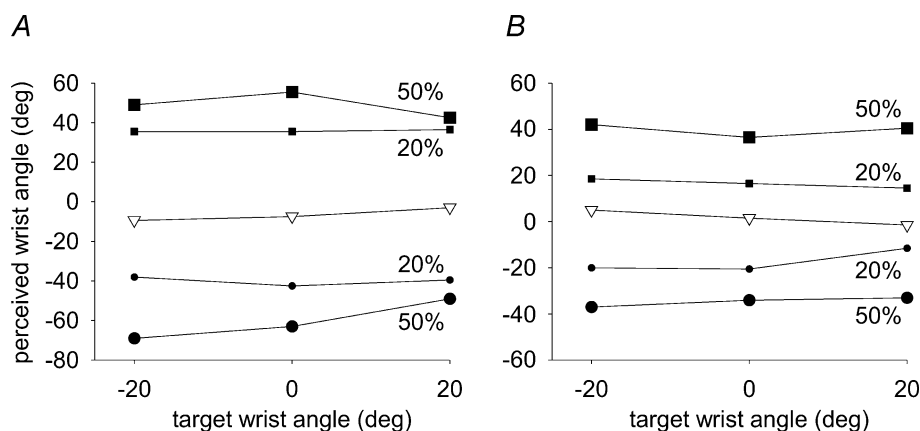
Figure 4. Greater flexion and extension efforts produce larger displacements of the phantom hand during combined anaesthesia and paralysis
Data from two subjects when the arm was paralysed and anaesthetized with a combination of lignocaine and ischaemia. The control position when no efforts were attempted is shown with open triangles. Low-level attempted efforts (at 20% maximum) resulted in perceived displacements of the hand (independent of starting position), in the direction of flexion for flexion efforts (small filled circles), and in the direction of extension for extension efforts (small filled squares). Higher-level efforts (at 50% maximum) produced larger illusory displacements in the position of the hand in flexion (large filled circles) and in extension (large filled squares). Each data point is the average of two trials.

but that such signals *in isolation* do not generate signals of movement or position (e.g. Goodwin *et al.* 1972; Matthews, 1982; Gandevia, 1996). This view has been based on detailed studies of attempted movements during anaesthesia and paralysis (Goodwin *et al.* 1972) and during local curarization (McCloskey & Torda, 1975). The reasons for the failure of the studies by Goodwin *et al.* (1972) and by McCloskey & Torda (1975) to demonstrate illusions of movement or attempted movement of unrestrained paralysed fingers is not clear. However, in both these studies, the attempted efforts were brief (< 1 s) and perhaps the subjects were not able to 'extract' an illusory signal in such a short time. In terms of mechanisms, demonstration of a consistent illusion is much more persuasive than a failure to find one.

Some previous results are consistent with an interaction between signals of motor command and afferent signals in judgements of position. For example, while Rymer & D'Almeida (1980) found errors in perceived position during the generation of an isometric (but not a non-isometric) contraction, they ascribed them to a central process involving inputs from Golgi tendon organs, as the errors did not change with fatigue. A similar distortion of position sense with elastic loads was observed by Watson *et al.* (1984), but who did not speculate about the precise mechanism. Further evidence for an effort-based contribution to position sense has recently been obtained (Walsh *et al.* 2004; Winter *et al.* 2005; Allen & Proske, 2005). However, these studies all involve forearm position matching in the presence of the force of gravity and it remains uncertain how the positional information is derived centrally, whether directly, or in terms of the perceived contraction force required to support the limb. No such ambiguity exists in the interpretation of the present results.

The present study does not reveal how a signal related to motor command interacts with feedback from the periphery to produce the sensations described here. As indicated earlier, ongoing judgements of position and movement may depend on a comparison between outflow and inflow signals. As voluntary contractions are usually produced via alpha–gamma co-activation (Vallbo, 1971), a central mechanism may exist to allow interpretation of muscle spindle signals taking some account of the movement commanded. In the terminology of von Holst (1954), the critical signal (ex-afference) is derived by comparison of the motor command (efference copy) with the total peripheral signal, taking into account the re-afference generated by the motor command through co-activation. Evidence consistent with the comparator hypothesis has been obtained in studies using whole-body neuromuscular paralysis in which all extrafusal contractions were abolished, but some intrafusal contractions may have persisted. Attempted movements produced

illusions of movement in the opposite direction to that intended (Gandevia *et al.* 1993*a*). That is, for movements in the direction of flexion, any sensation of flexion arising from the motor command was overwhelmed by a larger-than-normal spindle input signalling muscle lengthening since the attempted flexion was unaccompanied by the usual muscle shortening. In the present experiments, attempted movements produced illusions of position change in the direction of intended movement. As the spindle signal is absent during the block, it is less than expected, and this comparison could be interpreted as a change in position consistent with muscle shortening. However, other explanations are possible. It is our view that the current psychophysical experiments do not reveal whether subjects relied directly upon a signal related to motor output for their perceptual judgements or on a signal derived from the output of a comparator.

The present study has unmasked a previously undescribed role of signals of motor command in kinaesthesia. Furthermore, the observations have thrown new light on the neural processes underlying limb position sense and on the phenomenon of phantom limbs occurring after deafferentation and amputation.

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