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Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand

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1. In this study we tested the hypothesis that ensemble activity in human cutaneous sensory afferents evoked by the stretching of skin over and around the finger joints contributes to the conscious perception of movement of the fingers.
2. In nineteen normal adults, ensembles of cutaneous afferents were activated either by electrical stimulation, delivered through an array of electrodes on the dorsum of the hand and fingers, or by mechanical stretching of the skin over and around the joints. The stretching was applied through an array of threads stuck to the skin, in such a way as to avoid or minimize moving the underlying joints and to avoid applying pressure to underlying tendons and ligaments. Perceived movements were mimicked by voluntary movements of the fingers of the contralateral hand.
3. By way of comparison, kinaesthetic illusions were also evoked by activation of muscle receptors by vibration.
4. Illusions of movement were elicited with each type of stimulus. Electrical stimulation of skin afferents caused clear illusory movements in six out of seventeen subjects (35%), and borderline movement illusions in three out of the same seventeen subjects (total 9/17, 53%). Various other localized skin sensations were also reported. Skin stretch evoked movement illusions in eleven out of nineteen of subjects (58%). In all subjects who received both cutaneous stimuli, twelve out of seventeen (71%) reported some movement sensations with one or other of the stimulation techniques. Vibration tended to be the most reliable stimulus modality, eliciting illusory movements in fourteen out of sixteen subjects (88%).
5. Although the skin stretching technique did cause minute movements of nearby joints in several cases, these were monitored and shown in separate control experiments to be below perceptual threshold, and so the movement illusions could be safely attributed to the cutaneous afferent input evoked by skin stretch.
6. The results support the hypothesis that input from skin stretched during finger movement contributes to the conscious perception of the movement. Vibration-evoked muscle afferent input tended to be more reliable than the skin input in producing kinaesthetic illusions, though comparisons of the relative efficacy of the three techniques must be made with caution.

The study of human kinaesthetic sensibility has had a long and interesting history. Sherrington (1900) suggested a kinaesthetic role for 'sense organs in muscles, tendons and joints'. A rival theory which gained popularity suggested that 'corollary discharge' (Sperry, 1950) or 'efference copy' (von Holst, 1954) of the descending command dominated kinaesthesia. The notion of centrally generated kinaesthetic signals had its roots in Helmholtz's (1925) 'sensation of innervation' which derived from studies of eye movements. The 1950s and 1960s saw a renewed interest in receptors located in the joints, primarily because of studies suggesting that their firing profiles were ideal to signal joint position (Boyd & Roberts, 1953). But subsequently it was found that in fact few joint receptors fire over the full range of motion (Burgess & Clark, 1969; Ferrell, 1980). Attention quickly shifted back to the muscle receptors with the demonstration that excitation of muscle spindles by vibration induced illusory movements consistent with lengthening of the vibrated muscle (Eklund, 1972; Goodwin, McCloskey & Matthews, 1972). This finding has been corroborated many times since and it is now widely accepted that muscle spindles play an important role in kinaesthesia (Lackner &

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Levine, 1979; Roll & Vedel, 1982). Numerous reviews have been written on the topic (McCloskey, 1978; Matthews, 1982; Gandevia, 1996).

In contrast to muscle and joint receptors, cutaneous receptors have rarely been accorded a significant role in kinaesthesia, though the issue has been discussed for over a century (McCloskey, 1978). The question now is, to what extent does the central nervous system (CNS) extract proprioceptive and kinaesthetic information from the responses of cutaneous receptors to skin deformations accompanying movement. The terms proprioception and kinaesthesia are sometimes used synonymously, but proprioception has a more general connotation, encompassing all movement sensation, whether consciously perceived or not. Direct evidence that some cutaneous receptors can generate signals of a proprioceptive nature came from human neurographic recordings from receptors in the glabrous skin of the hand (Knibestöl & Vallbo, 1970; Hulliger, Nordh, Thelin & Vallbo, 1979). However, the response characteristics of these afferents during movements suggested that they could play only a small or facilitatory role in kinaesthesia (Hulliger *et al.* 1979; Burke, Gandevia & Macefield, 1988). In contrast, recent studies have indicated that receptors located in the hairy skin on the dorsum of the hand, particularly slowly adapting type-II (SAII) receptors, provide ideal signals from which to derive finger movements (Edin & Abbs, 1991; Edin, 1992; Grill & Hallett, 1995). There is also some evidence from animal studies that cutaneous signals are appropriate for proprioception (Appenteng, Lund & Seguin, 1982).

The fact that certain receptors generate signals from which kinaesthetic information can be derived does not of itself show that the CNS uses the signals in this way. However, indirect evidence for a kinaesthetic role for skin input came from studies in which finger movements were still detected after contributions from receptors in joint and muscle were removed either experimentally (Moberg, 1983; Ferrell, Gandevia & McCloskey, 1987; Clark, Grigg & Chapin, 1989) or as a result of reconstructive surgery (Moberg, 1972; but cf. McCloskey, 1978; McCloskey, Cross, Honner & Potter, 1983). Microstimulation of presumed single cutaneous afferents has only on rare occasions resulted in kinaesthetic illusions (Torebjörk & Ochoa, 1980; Vallbo, 1981; Torebjörk, Vallbo & Ochoa, 1987; Macefield, Gandevia & Burke, 1990). Torebjörk *et al.* (1987) concluded that spatial summation of input from SAII receptors may be required for conscious perception of their input. It should be noted that stimulation of presumed single muscle spindle afferents, the afferents most often implicated as the source of kinaesthetic information, has also rarely resulted in perception of movement (Macefield *et al.* 1990).

In two recent studies, selective stimulation to recruit ensembles of skin afferents was attempted. Gandevia (1995) reported briefly on the use of electrical stimulation to excite a population of non-muscle afferents in the human superficial radial nerve. Edin & Johansson (1995) stretched the dorsal and palmar skin of the index finger in human subjects. In both cases illusions of finger movement were evoked. Indeed the results suggested that, in certain circumstances, skin input may have precedence over the other proprioceptive modalities in the perception of movement and control of motor behaviour. Our study used elements of both of these recent investigations. However, we adopted a more quantitative approach, both in relation to the selective activation of afferents and in comparing the relative importance of cutaneous and non-cutaneous input in kinaesthesia. In all, we used three techniques to excite ensembles of afferents of the hand. Cutaneous input was evoked either by electrical stimulation delivered through an array of electrodes on the dorsum of the hand and fingers or by accurately controlled skin stretch. Muscle receptor input was evoked by vibration (Eklund, 1972; Goodwin *et al.* 1972), so that the kinaesthetic action of muscle and skin input could be compared. Part of this work has been reported elsewhere (Collins & Prochazka, 1995).

METHODS

Three sets of related experiments are described in this paper. The nineteen subjects (9 female, 10 male; 15–48 years old) had no history of neurological, allergic or skeletomotor disorders and were naive to the research hypotheses. Experiments were performed in accordance with the Declaration of Helsinki and were approved by the University of Alberta Hospitals Ethical Committee. All subjects gave their informed written consent to the procedures. Subjects were seated with their arms resting comfortably on a narrow table in front of them with their hands hanging relaxed over the edge. A screen blocked the subject's vision of sites distal to the mid-forearm. Stimuli were applied to the right hand and perceived movements were matched with the left hand. Subjects were told that the purpose of the experiment was to investigate the way people perceive sensations from the hands. They were asked to describe any sensations such as touch, pressure, movement, vibration and warmth associated with the stimuli. Movement was not emphasized. Experimental protocols are summarized in Table 1.

Experiment 1

The main aim was to characterize illusory movements evoked by electrical stimulation of the skin. A secondary aim was to characterize illusory movements evoked by mechanical stretching of the skin or vibration-elicited activity of muscle spindles. Seven subjects took part.

Electrical stimulation. Twelve pairs of 1 cm diameter brass electrodes with 0·63 mm thick conductive gel were stuck to the skin, in each case the anode being 1 cm distal to the cathode. Electrode pairs were located in three rows over the proximal interphalangeal (PIP) and the metacarpophalangeal (MCP) joints and the dorsum of the hand (electrode pairs 1–12 in Fig. 1*A*). A custom-built stimulator delivered independent, interleaved trains of 80 μs pulses through each electrode pair. Two personal computers with CED 1401 interfaces (Cambridge Electronic Design) were used to frequency modulate the pulse trains of all electrode pairs in phase at 0·3 Hz. Electrode pairs 1–8 were modulated through 5–650 Hz. Pairs 9–12 were modulated through 5–325 Hz, to mimic firing associated with smaller amounts of skin stretch. Perceptual

Table 1. Protocol summaries for the three experiments

	Experiment 1 (7)	Experiment 2 (11)	Experiment 3 (6)
Electrical stimulation			
Type	12 pairs, electrodes across PIP, MCP and dorsum of hand	12 pairs, electrodes across MCP and dorsum of hand	n.a.
Parameters	Sinusoidal; 5–650 Hz and 5–325 Hz	Sinusoidal; 3 ranges of stimulus frequencies	n.a.
Pattern	Full electrode array	Full array and index only	n.a.
Skin stretch			
Type	Elastic bands attached at 5–7 small spots on dorsum of index finger MCP joint	Elastic bands attached at 10–11 larger spots on dorsum of hand and across MCP	Threads at 2 spots across the index MCP; stretch appliedwith linear motor
Parameters	Medium stretch intensity	3 intensities of stretch	3 intensities of stretch
Pattern	Index finger only	All fingers and index only	Index MCP only
Vibration			
Location	Dorsum of hand	Dorsum of hand	n.a.
Frequency	100 Hz	70, 100, 130 Hz	n.a.
Movement quantification	Calculated from markers on the contralateral index finger on videotape	Calculated from length gauge across contralateral index MCP	Calculated from markers on both index fingers on videotape; movement detection threshold also determined

The number of subjects is given in parentheses. n.a., not applicable.

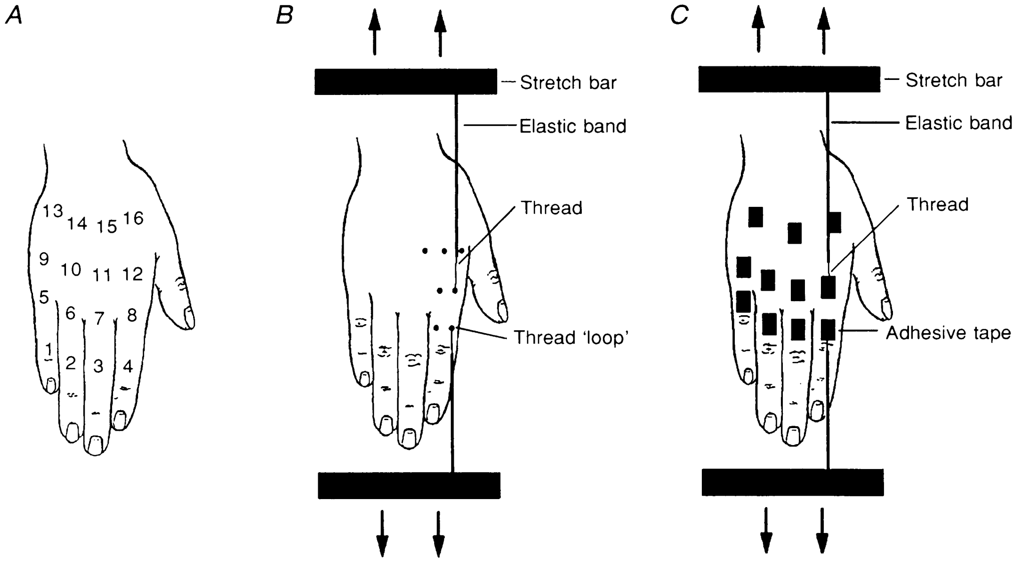

Figure 1. Diagram of the experimental hand for experiments 1 and 2

A, electrode placements for the electrical stimulation. Each number represents an electrode pair. Numbers are consistent with those in the text and in Table 2. For each pair, the cathode was just proximal to the number and the anode was just distal (5 mm separation). Experiment 1, electrode pairs 1–12. Experiment 2, pairs 5–16. *B*, schematic diagram of the skin stretch technique used in experiment 1. Each dot represents a site at which the looped end of a short thread was stuck to the skin. Elastic bands were attached to each thread, shown twice only for clarity. Elastic bands were clamped to the stretch bars and the skin was stretched when the bars were moved away from each other. *C*, schematic diagram of the skin stretch technique used in experiment 2. Filled rectangles indicate patches of adhesive tape securing threads to skin.

Table 2. Electrical stimulation protocols for experiment 2

Electrode pair no.	Stimulus combination: All low	All medium	All high	Index low	Index medium	Index high
5	5–200	5–450	5–700	Off	Off	Off
6	5–200	5–450	5–700	Off	Off	Off
7	5–200	5–450	5–700	Off	Off	Off
8	5–200	5–450	5–700	5–200	5–450	5–700
9	5–150	5–350	5–500	Off	Off	Off
10	5–150	5–350	5–500	5–125	5–250	5–400
11	5–150	5–350	5–500	5–150	5–250	5–500
12	5–150	5–350	5–500	5–175	5–400	5–600
13	5–100	5–250	5–300	5–75	5–200	5–300
14	5–100	5–250	5–300	5–100	5–250	5–350
15	5–100	5–250	5–300	5–125	5–250	5–400
16	5–100	5–250	5–300	5–150	5–350	5–500

Frequency ranges (Hz) allocated to each electrode pair for each stimulus combination. See Fig. 1*A* for electrode locations.

threshold was determined separately for each electrode pair using a graded 300 Hz pulse train. Then with all twelve electrode pairs active, pulse amplitudes were individually increased to levels somewhat below those which subjects considered uncomfortable. If the stimulation caused overt muscle twitches the trial was discontinued. Stimulation was delivered in three to six blocks of fifteen to seventy-five consecutive cycles.

Skin stretch. Loops of thread about 4 mm in diameter soaked in cyanoacrylate glue were stuck to the skin at five to seven locations proximal and distal to the index finger MCP joint (see Fig. 1*B*). The threads were tied to elastic bands which were fixed to stretch bars held by the experimenter on either side of the MCP joint. Movements of the stretch bars away from each other stretched the skin over the MCP joint in an even and balanced manner (see Fig. 1*B*). Thicker pairs of elastic bands (*ca* 60 N m^{-1} compliance) were used at the two locations on either side of the MCP joints and thinner bands (*ca* 20 N m^{-1} compliance) were used at the more proximal sites to provide a graded skin stretch centred over the MCP joint. The stretch was delivered manually in a quasi-sinusoidal fashion at about 0·3 Hz so that the strain of the skin was similar to that seen during finger flexion of about 45 deg from neutral. Each subject received a block of ten to twenty-five consecutive stretches. Stretch was applied so as to minimize movement of the hand or fingers, which was examined in video films (see below).

Vibration. Small-amplitude 100 Hz vibration was applied to tendons in the dorsum of the hand. The 10 mm diameter tip of the custom-built vibrator was applied to sites that were the most effective in creating illusions of index finger flexion. Typically this was just proximal and slightly medial to the index finger MCP joint, over the tendons of the extensor indicis and extensor digitorum muscles (between electrodes 11 and 12 in Fig. 1*A*). The vibrator was turned on and off at about 0·3 Hz. Each subject received a block of trials of ten to twenty-five consecutive cycles of stimulation. If the vibration evoked overt reflex-mediated muscle twitches, the trial was discontinued.

Experiment 2

Experiment 1 was repeated using more controlled stimuli to allow comparisons of the relative strengths of the effects produced by the three stimulus modalities. Stimuli were delivered in equal blocks of trials and at three intensities chosen to encompass the presumed physiological range for each modality. We also examined the effects on illusory movement of the spatial pattern of electrical stimulation and skin stretch. Two spatial patterns were used for each modality, one to mimic flexion of all the fingers and the other flexion of the index finger only. Eleven subjects participated. Each experimental session was conducted in three randomized blocks of trials, each involving a given stimulus modality. Matching movements of the left index finger were monitored with a silicone rubber length gauge attached across the MCP joint. These data along with the time course of electrical, stretch and vibratory stimuli were sampled and stored using a CED 1401 interface and computer system running customized software.

Electrical stimulation. Twelve electrode pairs were stuck to the dorsum of the hand in three rows, the most distal row spanning the MCP joints of each finger (electrode pairs 5–16 in Fig. 1*A*). Two spatial patterns of stimulation were used. Spatial pattern 1: frequency-modulated stimulation (0·3 Hz) was delivered in-phase through all twelve electrode pairs to elicit illusions of rhythmical flexion of all the fingers. Spatial pattern 2: frequency-modulated stimulation (0·3 Hz) was applied in-phase through electrode pairs 8 and 10–16 (Fig. 1*A*) to elicit illusions of movement of the index finger only. Table 2 shows the three frequency ranges used (low, medium and high) and their allocations to different electrode pairs. We used a video, kindly supplied by Dr B. B. Edin showing skin strain at a matrix of points on the dorsum of the hand as a guide in selecting the range of stimulus frequencies at the different electrodes. We wanted to ensure that our highest stimulation rates matched or exceeded natural firing in the fastest possible finger movements. In freely moving cats, skin afferents can fire in excess of 700 s^{-1} (Trend, 1987; authors' personal observations). We therefore selected 5–700 s^{-1} for our largest frequency range, a maximum well above that of skin afferents recorded neurographically during slow finger movements (Edin & Abbs, 1991) or during skin stretch corresponding to fast finger movements (Edin, 1992). Each combination of stimulus pattern and intensity was delivered in two to four successive trials of fifteen consecutive cycles of stimulation. The presentation order of the six combinations within a block was randomized across subjects.

Skin stretch. The skin stretch apparatus was attached to the skin at ten to eleven sites on the dorsum of the hand (Fig. 1*C*) using pieces of adhesive tape (about 12 mm × 16 mm). Two spatial patterns of manually applied skin stretch were used. Spatial pattern 1: the stretch was bi-directional away from the MCP joints, using all the pieces of adhesive tape, to mimic skin stretch associated with movement of all the fingers. Spatial pattern 2: stretch was applied through four to five pieces of tape on either side of the index finger MCP joint, to mimic skin stretch associated with movement of the index finger only. For each pattern the skin was stretched by amounts intended to mimic small, medium and large flexions of the MCP joints. The corresponding skin strains were estimated to be in the range 2–8% (see Experiment 3, Skin stretch in Results). Each combination of spatial pattern and intensity was delivered in two to four successive trials of ten to fifteen consecutive cycles. The presentation order of the six combinations within a block was randomized across subjects. A length gauge was used to monitor the time course of the movements of the proximal stretch bar.

Vibration. The optimal stimulation sites to evoke illusions of index finger flexion were determined as in experiment 1. The vibrator was then clamped in place with a retort stand and turned on and off at approximately 0·3 Hz. Vibration at 70, 100 and 130 Hz was delivered in randomized blocks of two to four successive trials, each consisting of ten to fifteen consecutive cycles of stimulation.

Experiment 3

The skin stretch trials in experiments 1 and 2, while often successful in producing movement illusions, involved manual stretching that was variable and difficult to quantify. Moreover, we found that it was difficult to stretch the skin without moving the fingers albeit very slightly. Our aims were to: (a) apply accurately controlled skin stretch; (b) quantify the magnitude and time course of the stretch; (c) minimize and quantify joint movements evoked by the stretch; and (d) establish the subjects' ability to detect comparable joint movements. Six subjects participated, five of whom had taken part in experiment 1 or 2. The sixth subject had been involved in pilot studies before experiments 1 and 2. Subjects were chosen on the basis that in previous skin stretch trials, three had reported illusory movements (subjects S6, S17 and S19 in Table 3) and three had not (S2, S5 and S8).

Subjects were told that the experiment was a continuation of the study on the perception of sensations from the hands, but they were not informed that skin stretch or finger movement trials were involved. They were told that if they perceived any sensations they should respond as in experiments 1 and 2. Skin stretch and joint movements were each delivered at three amplitudes. All trials of one amplitude were delivered within a single block of approximately eighty consecutive cycles. Blocks were alternated between skin

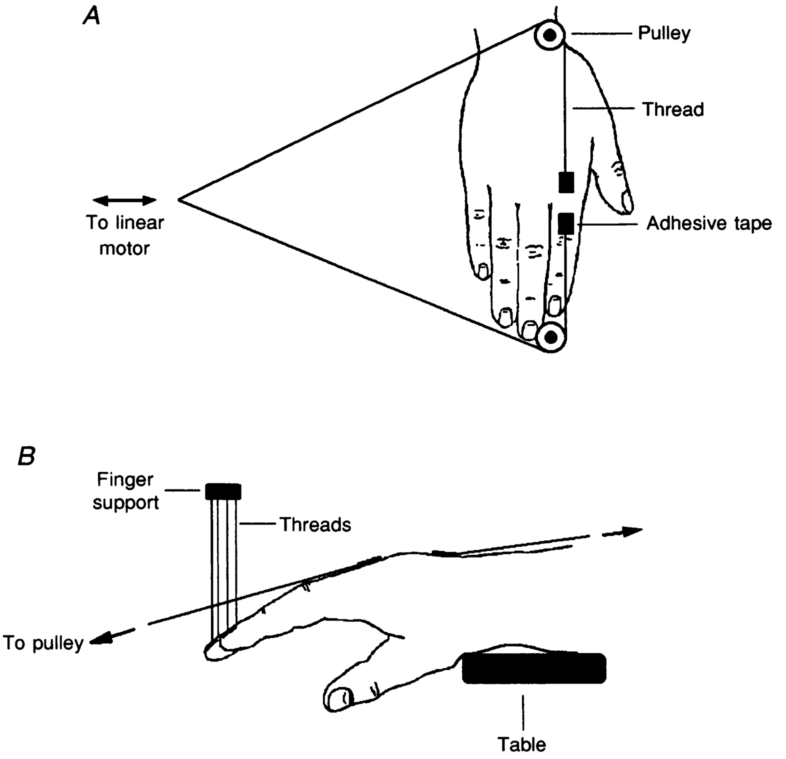

Figure 2. Diagram of the skin stretch technique used in experiment 3

A, top view showing the threads attached to skin by patches of adhesive tape (filled rectangles). Each thread was connected via a pulley to the shaft of a linear servomotor. This provided precise, equal and opposite sinusoidal stretches to the skin. *B*, side view showing the position of the experimental hand and other threads supporting the fingers from above (adapted from Vallbo *et al.* 1995).

stretch and finger movement and presentation order of the small, medium and large amplitudes was randomized across subjects.

Skin stretch was applied via two pieces of adhesive tape (*ca* 12 mm × 16 mm) stuck to the skin just proximal and distal to the index finger MCP joint (Fig. 2*A*). During skin stretch trials threads attached to the tape were connected via pulleys to a feedback-controlled electromagnetic length servo which provided 0·3 Hz sinusoidal stretches of different amplitudes. To minimize actual joint movement caused by the applied skin stretch, the fingers of the right hand were suspended from above by threads stuck to the fingernails with cyanoacrylate glue (Fig. 2*B*). The pulleys were carefully positioned so that the skin stretch was well balanced and produced minimal movements of the finger. Despite these precautions, minute joint movements were usually observed. They were measured from video films as described below and compared with the perceptual thresholds determined as follows. The suspension thread attached to the nail of the index finger was connected to the servomotor to permit application of precisely controlled 0·3 Hz sinusoidal movements at the MCP joint. Care was taken to ensure that subjects were unaware of whether skin stretch or real finger movements were involved in a trial. Three movement amplitudes were applied that encompassed the detection threshold.

Data collection and statistical analysis

All sessions were videotaped (Sony Video Camera, Panasonic OmniMovie HQ). Subjects matched with their left index finger the magnitude and time course of illusory movements of the right index finger. Images were digitized *post hoc* (Video Blaster/Video Kit 1.20) and movements of ink dots or self-adhesive dots on the medial side of the left and right index fingers were quantified using image analysis software (SigmaScan/Image 1.20.09). In experiment 3 a Sharp Viewcam was used for close-up videotaping of the dots, giving a spatial resolution of 80 μm, as determined by filming movements of a linear servomotor. For a dot located at the distal interphalangeal (DIP) joint, this is equivalent to rotation of the MCP joint of 0·1 deg or less. Skin strain was calculated from digitized, close-up images of a 12 mm × 12 mm grid (2 mm between lines) stamped on the skin over the right index finger MCP joint. Between twelve and twenty-four measurements were made from each of the stretched and unstretched grid images for each calculation.

To evaluate the relative strengths of each technique in evoking illusory movements the ten largest movements at the index finger MCP joint, regardless of spatial pattern or intensity of the stimulus or the resultant movement direction, were averaged together for each subject in experiments 1 and 2 (see Table 3). In cases where fewer than ten illusory movements were recorded, all the available movements were used for the mean. These data were tested using the ANOVA analyses described below. The relative strengths of the techniques in producing illusions were also tested using McNemar's test to make pairwise comparisons between the proportions of subjects who perceived illusory movements for each technique. Within a subject the direction of the perceived movement was consistent, i.e. movements contributing to the means for a given subject were always of the same direction. Tests for a significant effect of spatial pattern and/or intensity of stimulation on movement magnitudes were conducted on the mean movement amplitudes for each combination of pattern and intensity for subjects in experiment 2 who reported illusory movements. Statistical tests across subjects were conducted using one- and two-way repeated measures analysis of variance (ANOVA) followed by the Student–Newman–Keuls *post hoc* multiple comparisons test to identify significant differences. When the data were found not to be normally distributed and/or of equal variance analyses were conducted using Friedman's ANOVA on ranks followed by Wilcoxon signed rank (Bonferroni) or Student's t (when pairwise comparisons were normally distributed) tests. Comparison of illusory movement magnitudes between techniques within a subject were conducted using Student's t tests or Mann–Whitney U tests (when tests for normality or equal variance failed) on the data in Table 3. Statistical significance was accepted when $P < 0{\cdot}05$.

RESULTS

The main aim of this study was to evoke illusory movements by activating predominantly skin receptors or predominantly muscle receptors and to compare the strengths of the illusions. Electrical stimulation and skin stretch were used to excite skin receptors and vibration was used to excite muscle receptors in experiments 1 and 2. We first present the characteristics and relative strengths of the movement illusions evoked by each technique using data from all the subjects in experiments 1 and 2. Next we describe the relationship between the spatial pattern and intensity of stimulation on the illusory movements as examined in experiment 2. Finally, the results of experiment 3, which focused on the skin stretch technique, are described.

1. Movement characteristics and relative strengths (experiments 1 and 2)

In this section we describe, first qualitatively and then quantitatively, the illusory movements evoked by each technique. It should be noted that all illusions involved the perception of smooth movements, temporally linked to the cyclical application of the stimuli (with one exception: see Electrical stimulation below). First we will concentrate on movements of the index fingers. Movements of the other fingers are described in section 2 below. Mean movement magnitudes used for this analysis, along with movement direction and the number of movements comprising each mean, are given in Table 3. Subject numbers in Table 3 reflect the chronological order of participation in the study and are subsequently used in the text to identify subjects.

Electrical stimulation. Sinusoidal variations in stimulus frequency were delivered through an array of electrodes stuck to the dorsum of the right hand. One subject's data (S5) are omitted from this section because the stimulus could not be applied without an accompanying motor response. Average stimulus intensity across the remaining seventeen subjects was 1·34 ± 0·13 times perceptual threshold (mean ± 1 s.d.).

Electrical stimulation evoked illusory movements in six out of seventeen subjects (35%, Fig. 3*A*). McNemar's test identified that this proportion was not significantly different to that for the skin stretch technique ($P = 0{\cdot}289$) but was significantly smaller than that for vibration ($P = 0{\cdot}012$). As we posited, the most common illusory movement (5/6 subjects) was flexion at the index finger MCP joint as stimulus frequency increased (see Table 3). An example of this is shown in the raw data in Fig. 4*A* for three cycles of stimulation through the whole electrode array over the low frequency range ('All low' stimulus combination in Table 2). These data are from subject S14 who perceived movement during all three stimuli. Subject S3 perceived a slight extension of the MCP joint during increasing stimulus frequency, but found the movement direction 'difficult to determine'. Movement characteristics within a subject were consistent within an experimental session. Perceived flexion of the PIP and DIP joints generally matched that of the MCP joint, but occasionally a large illusory flexion at the PIP joint was accompanied by a small illusory movement at the MCP joint (e.g. subject S6). One subject (S10) reported a paradoxical sense of position change without a sense of movement; in several trials the perception was of a static flexion of all the fingers as if in a grasp throughout several cycles of stimulation. Four subjects (S9, S13, S14 and S16) occasionally felt 'as though their fingers should be moving' but knew that they were not.

The magnitude of the illusory movements at the MCP joint evoked by electrical stimulation was generally small. Mean amplitude across the six subjects who clearly perceived movement during electrical stimulation was 11·3 ± 16·6 deg (range, 1·0–44·8 deg); see Table 3. Five of these six subjects perceived movements smaller than 10 deg during electrical stimulation (see Fig. 3*B*). ANOVA identified no significant difference between electrical stimulation and skin stretch ($P = 0{\cdot}052$) but electrical stimulation was significantly less effective than vibration in evoking illusory movements ($P = 0{\cdot}009$). Of the three subjects who perceived illusory movements with both electrical stimulation and vibration, significantly larger illusory movements were evoked by electrical stimulation in one subject (S2) and by vibration in the other two (S10 and S14).

Electrical stimulation also evoked tactile illusions of a non-kinaesthetic nature. All subjects perceived 'pins and needles' sensations under the stimulating electrodes. Pressure was the next most frequently reported tactile sensation. Descriptions also included a squeezing of the fingers 'like a firm hand-shake', a pushing down on the dorsum of the hand, rubbing, brushing or scraping across the skin, touch, tapping, flutter, warmth, cold and occasional numbness. A sensation of skin tightening was also frequently reported yet this was not always associated with sensations of movement. Three subjects described some of the sensations as being similar to those evoked by actual skin stretch.

Skin stretch. Threads stuck to the dorsum of the hand were used to manually stretch areas of skin over the MCP joints and hand. This was effective in creating the illusion of movement in ten out of eighteen subjects (56%) tested in experiments 1 and 2 (see Fig. 3). This proportion was not significantly different from that for electrical stimulation ($P = 0{\cdot}289$) or vibration ($P = 0{\cdot}07$). Raw data for three cycles of small-amplitude skin stretch across the whole hand

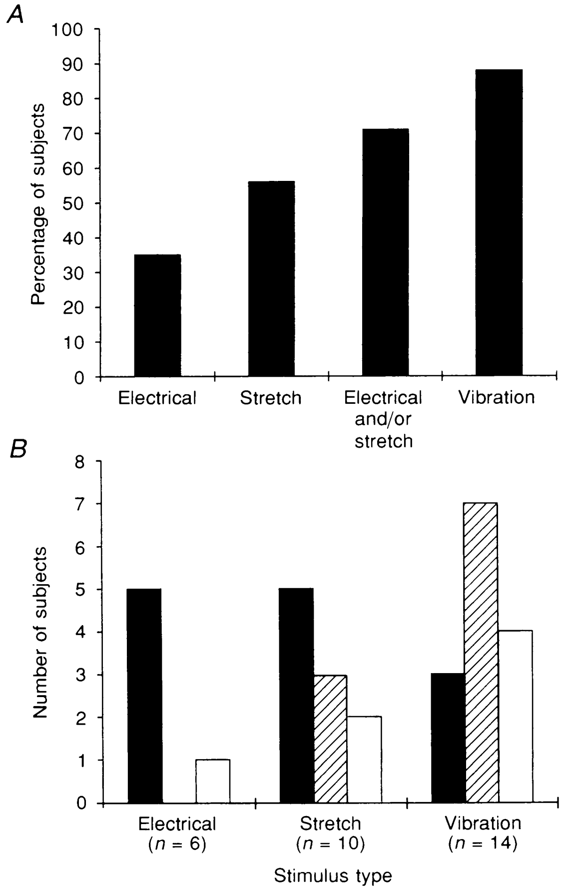

Figure 3. Summary of results for experiments 1 and 2

A, percentage of subjects who perceived illusory movements of the fingers for each type of stimulation. *B*, number of subjects who perceived small (0–9 deg, ■), medium (10–19 deg, ▨) and large (20+ deg, □) illusory movements evoked by each technique.

are shown in Fig. 4*B* for subject S14 who perceived illusory movement from all three types of stimuli. This subject reported illusions of finger flexion consistent with our hypothesis. However, most subjects (7/10) perceived extension of the MCP during periods of skin stretch. As with electrical stimulation, responses tended to be variable between subjects, though relatively stable for a given subject. Movements during illusory MCP joint extension were usually restricted to that joint, though some subjects reported concomitant flexion or extension of the more distal joints. The three subjects who perceived MCP flexion consistently reported concomitant flexion at the PIP joint. In one case a slight abduction of the MCP joint was perceived.

Illusory movement amplitudes evoked by the skin stretch tended to be intermediate between those evoked by electrical stimulation and vibration. Mean movement amplitude across the ten subjects who perceived movements was 13·8 ± 9·7 deg (range, 3·7–31·4 deg) as shown in Table 3. Movement amplitudes were categorized as small (0–9 deg), medium (10–19 deg) and large (20+ deg) and are displayed graphically in Fig. 3*B*. ANOVA identified no significant difference between skin stretch and electrical stimulation ($P = 0{\cdot}052$) and a significantly smaller effect of the skin stretch when compared with vibratory-evoked illusions ($P = 0{\cdot}02$). Of the seven subjects who perceived illusory movements with both skin stretch and vibration, significantly larger illusory movements were evoked by skin stretch in three subjects (S10, S14 and S17) and by vibration in two subjects (S13 and S15). Movement magnitudes were not significantly different in the other two (S1 and S4).

Close inspection of the filmed sessions revealed some trials in which very small amplitude 'real' movements of the fingers were generated by the skin stretch. In about half of the cases these movements were so small that their direction

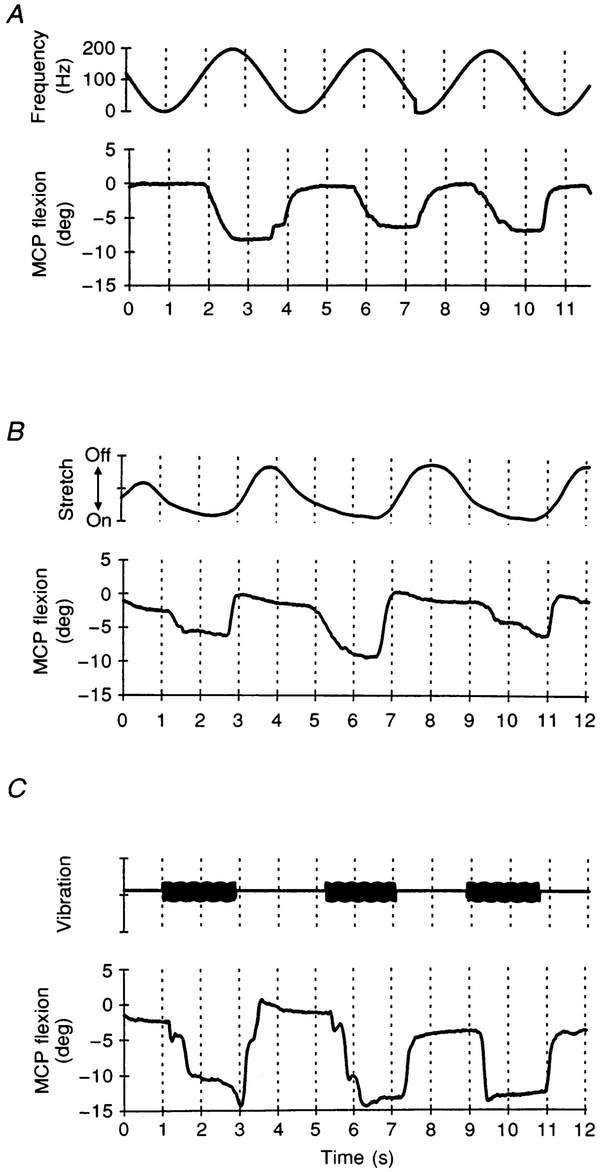

Figure 4. Illusory movements evoked by all three techniques in a single subject

These raw data show three cycles of each type of stimulation for subject S14. *A*, illusory movements of the index finger evoked by electrical stimulation through the full electrode array over the low frequency range. Top trace, time course of stimulus frequency; bottom trace, movements of the left index finger matching the perceived illusory movement. Stimulus frequencies shown are for electrode pairs over the MCP joints (pairs 5–8 in Table 2). *B*, illusory movements of the index finger evoked by small-amplitude skin stretch delivered across the whole hand (Fig. 1*C*, all patches). Top, time course of the skin stretch; bottom, matched illusory movement. *C*, illusory movements of the index finger evoked by bursts of 70 Hz vibration. Top, time course of vibration; bottom, matched illusory movement.

Table 3. Mean amplitudes of the largest illusory movements evoked by each technique for each subject in experiments 1 and 2

	Electrical stimulation		Skin stretch		Vibration	
Subject	Index MCP (deg)	Direction	Index MCP (deg)	Direction	Index MCP (deg)	Direction
Expt 1						
S1	0·00 ± 0·00 (10)	None	13·6 ± 14·1 (2)	Extension	8·4 ± 4·4 (5)	Extension
S2	44·8 ± 14·9 (10)	Flexion	0·00 ± 0·00 (10)	None	25·8 ± 8·9 (8)	Flexion
S3	8·6 ± 2·9 (10)	Extension	9·4 ± 5·1 (4)	Extension	n.a.	n.a.
S4	0·00 ± 0·00 (10)	None	12·8 ± 3·5 (3)	Extension	14·9 ± 5·5 (5)	Flexion
S5	n.a.	n.a.	0·00 ± 0·00 (10)	None	38·9 ± 16·3 (4)	Flexion
S6	3·4 ± 3·5 (6)	Flexion	31·4 ± 8·0 (10)	Extension	n.a.	n.a.
S7	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None	12·2 ± 6·5 (4)	Flexion
Expt 2						
S8	1·0 ± 0·4 (2)	Flexion	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None
S9	0·00 ± 0·00 (10)	None	6·4 ± 0·9 (2)	Extension	0·00 ± 0·00 (10)	None
S10	3·2 ± 0·9 (10)	Flexion	7·5 ± 0·6 (10)	Extension	6·2 ± 0·9 (10)	Flexion
S11	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None	7·1 ± 0·6 (10)	Flexion
S12	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None	11·7 ± 1·7 (10)	Flexion
S13	0·00 ± 0·00 (10)	None	6·6 ± 4·1 (7)	Extension	12·7 ± 2·1 (10)	Flexion
S14	6·7 ± 1·5 (10)	Flexion	15·9 ± 1·0 (10)	Flexion	10·0 ± 2·5 (10)	Flexion
S15	0·00 ± 0·00 (10)	None	3·7 ± 1·7 (10)	Flexion	13·2 ± 2·1 (10)	Flexion
S16	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None	28·5 ± 3·9 (10)	Flexion
S17	0·00 ± 0·00 (10)	None	30·3 ± 1·9 (10)	Flexion	28·7 ± 1·3 (10)	Flexion
S18	0·00 ± 0·00 (10)	None	0·00 ± 0·00 (10)	None	15·1 ± 1·9 (10)	Flexion
Mean	11·3 ± 16·6 (6)	Flexion	13·8 ± 9·7 (10)	Extension	16·7 ± 9·8 (14)	Flexion

Results are given as means ± S.D. with *n* given in parentheses.

could not be reliably discerned from the video images. In the remainder, small flexion, extension or lateral movements of the finger were distinguished during skin stretch. It should be noted that such movements were present both when illusory movements were reported and when they were not. Furthermore, the amplitudes of the 'real' movements were always much smaller than those of the corresponding illusory movements (i.e. contralateral matching movements).

Vibration. Vibration was applied to the finger extensor tendons on the dorsum of the hand just proximal to the index finger MCP joint. In two subjects (S3 and S6) this consistently caused reflexive movements of the fingers and so their data were discarded. Vibration evoked illusory movements in fourteen of sixteen subjects (88%), which, as mentioned previously, was a significantly greater proportion than for electrical stimulation but not for skin stretch (see Fig. 3*A*). Responses to vibration were the most consistent within and between subjects. All but one of the subjects (S1) reported flexion of the MCP joint during extensor tendon vibration. This is to be expected, given that extensor muscle spindles increase their firing during passive flexion movements (Al-Falahe, Nagaoka & Vallbo, 1990). An example of illusory movements evoked by vibration is shown in Fig. 4*C*: subject S14, three cycles of vibration at 70 Hz. Perceived flexion of the MCP joint was generally accompanied by perceived flexion of the two more distal joints.

As well as evoking illusory movements in the largest number of subjects, vibration-evoked illusory movements tended to be of larger amplitude than did the other two techniques, as shown in Fig. 3*B*. ANOVA revealed that vibration was significantly more effective than either of the other two techniques at evoking illusory movements (see above). Mean amplitude across the fourteen subjects who perceived movements was 16·7 ± 9·8 deg (range, 6·2–38·9 deg); see Table 3. However, as indicated above, when illusory movements were evoked by skin stimulation *and* vibration, within subject analysis revealed that larger movements were evoked by skin stimulation in three subjects, by vibration in two subjects and movement magnitudes were not significantly different in the other two.

Efficacy of the cutaneous stimuli. Electrical stimulation and skin stretch both evoked illusory movements but the difference in their efficacy was not statistically significant (see above). It should be noted that nearly three-quarters of the subjects (12/17, 71%) responded to at least one of the cutaneous stimuli and about a quarter (4/17, 24%) responded to both (see Fig. 3*A*).

2. Dependence of movement illusions on stimulus level and pattern (experiment 2)

In experiment 2 all stimuli were delivered at three intensities, to cover the range which evoked maximal illusory movements for each subject. In addition, two patterns of electrical and skin stretch stimulation were used, one to mimic flexion of all the fingers and the other flexion of the index finger only.

The size of illusory movements of the index finger MCP joint reported by subjects was not significantly correlated with stimulus amplitude (electrical pulse frequency range, skin strain amplitude or vibration frequency) for any of the modalities studied ($P > 0{\cdot}05$). Similarly, the spatial pattern of electrical and skin stretch stimulation had no statistically significant effect on the magnitude of the illusory movement at the index finger MCP joint ($P > 0{\cdot}05$). However, inspection of the videotaped sessions revealed that in some cases the pattern of stimulation appeared to have an effect on illusory movement of the other fingers.

Electrical stimulation was only effective at evoking illusory movements in three out of eleven subjects in experiment 2. Two spatial patterns of stimulation were used: the first to evoke illusions in all the fingers and the second to evoke illusions in the index finger only. In either case the three responding subjects felt most movement in the index finger, as judged from the contralateral matching movements, but smaller movements of the other fingers were also perceived. There were cases where the illusory movements corresponded to the spatial pattern of stimulation (i.e. all fingers or index finger only), but generally the contralateral matching movements were surprisingly similar for the two spatial patterns.

Illusory movements of the index finger MCP joint were not significantly different for the two spatial patterns of skin stretch, though illusory movements of the other fingers did show some correlation. This was most pronounced in subject S17, so a second length gauge was fitted across the MCP joint of his third finger to record this effect (Fig. 5). Figure 5*A* depicts the contralateral matching movements when medium amplitude skin stretch was applied over all the MCP joints and the dorsum of the test hand. The subject perceived that all the joints of all the fingers flexed as if in a grasping movement. When medium amplitude skin stretch was applied only around the index finger the resultant

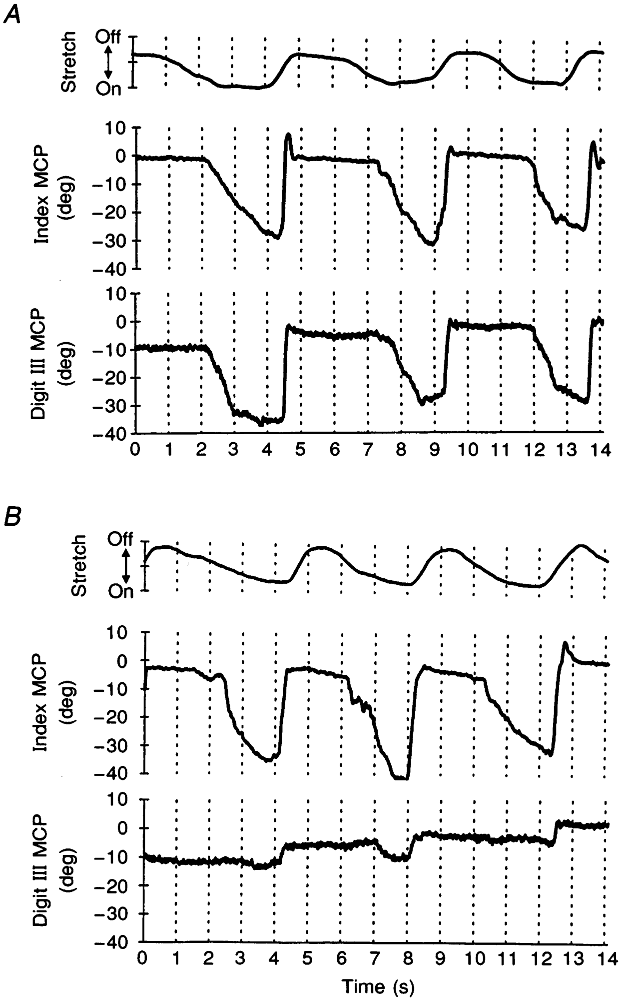

Figure 5. Illusory movements evoked by the two spatial patterns of skin stretch

Raw data from subject S17 who had length gauges across both the index finger and digit III MCP joints. *A*, skin stretch (top trace) and resultant illusory movements of the fingers (lower traces) for medium amplitude skin stretch through all the pieces of adhesive tape in Fig. 1*C*. *B*, skin stretch (top trace) and resultant illusory movements of the fingers (lower traces) for medium amplitude skin stretch through the pieces of adhesive tape over the index finger only.

illusory movement was localized to flexion of the joints of that finger and to a lesser extent of the adjacent finger (see Fig. 5*B*). Similar but less extreme dependence on stimulus pattern was observed in other subjects.

Vibration was applied at points which best evoked illusions of index finger flexion. However, some subjects perceived movements of the adjacent middle finger. The lack of a significant effect of vibration frequency on the resultant illusory movements is contrary to previous results (Roll & Vedel, 1982) and may be due to a lack of precise control over the pressure of application of the vibration in our trials.

3. Accurately controlled skin stretch (experiment 3)

Actual movement detection and matching. In most cases it was difficult to impose skin stretch without causing concomitant small movements of the finger. To determine if these real movements could be detected by the subjects we purposely applied similar movements through a thread stuck to the subject's fingernail, using a linear electromagnetic servo as described in Methods. Subjects were requested to match 0·3 Hz sinusoidal movements of the right index finger MCP joint of three amplitudes. The mean amplitudes of these imposed movements across all six subjects and the attempts to match them are shown graphically in Fig. 6*A*. The mean amplitude of the small movement was 0·21 ± 0·03 deg (range, 0·18–0·25 deg) and this was below the detection threshold of all the subjects. The amplitude of the medium-sized movement was increased until the subject first sensed the movement. Mean amplitude of these movements, averaged across the six subjects, was 0·41 ± 0·13 deg (range, 0·29–0·64 deg). The highest detection threshold was seen in the oldest subject, in accord with recent reports of reductions in kinaesthetic sensitivity with age (Gilsing *et al.* 1995). Five of the six subjects overestimated this movement amplitude when trying to match it with movements of the contralateral index finger, though the differences were not statistically significant ($P = 0{\cdot}052$). Mean amplitude of the matching movements of the left index finger MCP joint was 2·71 ± 2·20 deg (range, 0·30–6·06 deg). All subjects detected the large amplitude movements (2·77 ± 0·80 deg; range, 1·24–3·51 deg). This amplitude of movement was significantly overestimated by all subjects ($P = 0{\cdot}008$). Mean matching movements of the left index finger MCP joint for these large movements was 7·25 ± 3·14 deg (range, 3·27–11·28 deg). Across all subjects the small, medium and large movements of the right index finger had mean peak movement velocities at the MCP joint of 0·4, 0·8 and 2·6 deg s^{-1}, respectively.

With few exceptions subjects were accurate at matching the direction of the movement and were able to identify that the movement was restricted to the index finger MCP joint. However, there were cases, especially for the movements just above detection threshold, where matching movements

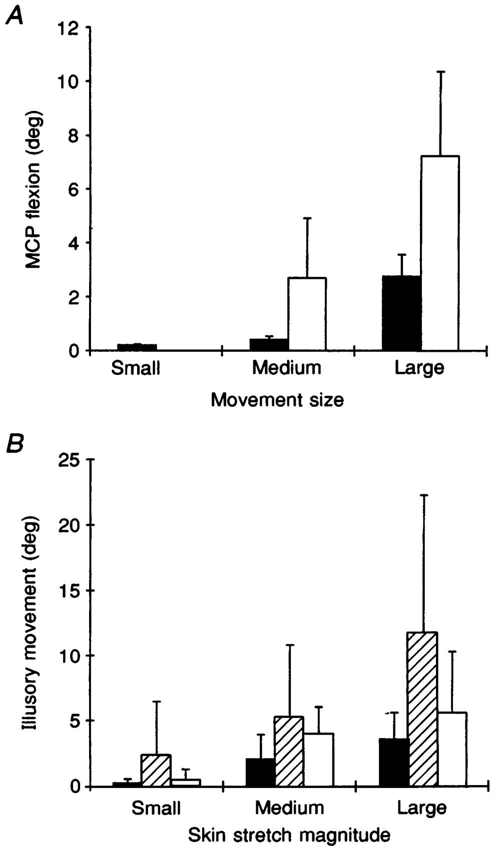

Figure 6. Results summary for experiment 3

A, mean data across the six subjects for movement detection and matching trials. ■, mean amplitude of the actual movement at the right index finger MCP joint; □, mean amplitude of the movement at the left index finger MCP joint when subjects attempted to match the movement of the right index finger. *B*, mean amplitudes of illusory movements of the different joints of the index finger evoked by skin stretch over MCP joint of the index finger. ■, MCP joint; ▨, PIP joint; □, DIP joint. Mean data from the three subjects who perceived illusory movements for small (2·2 % strain), medium (4·9 % strain) and large (7·7 % strain) amplitudes of skin stretch. Error bars, standard deviations of mean.

occasionally drifted out of phase with the actual movement. Subjects would then comment that they knew that the finger was moving but had difficulty identifying the direction or matching the amplitude. Such difficulty in determining the direction of movements close to detection threshold has been reported previously (Hall & McCloskey, 1983). Also, the matching movements of two subjects included some movement at the PIP joint and one of these subjects occasionally reported a scissoring movement at the MCP joints of the first two fingers.

Skin stretch. The skin over the right index finger MCP joint was stretched at three amplitudes. The results of these trials were consistent with those obtained from the same subjects in earlier experiments; illusory movements were only evoked in the three subjects who had previously reported them. Also, even though the characteristics of the illusory movements were quite different between these three subjects, within a subject movement characteristics were consistent with those perceived in the earlier experiments. One subject reported large flexions of the MCP and PIP joints of the index finger. Another reported extension at these two joints of the index finger with occasional similar movements of the next finger. The third subject reported a slight flexion and abduction at the index finger MCP joint. All illusory movements smoothly followed the cyclical application of the stretch, beginning during periods of skin stretch and returning to the rest position when the stretch was not applied.

The amplitude of the illusory movements, averaged across the three subjects who perceived them, tended to become progressively larger as the amplitude of the stretch increased (see Fig. 6*B*). However, this tendency failed to reach statistical significance ($P = 0{\cdot}08$).

The amplitude of the skin stretch was calculated for each skin stretch trial from digitized images of the grid patterns stamped over the MCP joint. The skin stretch amplitudes, expressed as a percentage of unstretched values and averaged across the six subjects were $2{\cdot}2 \pm 1{\cdot}8$, $4{\cdot}9 \pm 4{\cdot}4$ and $7{\cdot}7 \pm 5{\cdot}4$%, for the small, medium and large stretch trials, respectively. These means were significantly different across all six subjects ($P = 0{\cdot}003$) and no significant differences were identified in the amplitude of skin stretch between the three subjects who perceived movements and the three who did not ($P = 0{\cdot}995$).

In many trials the skin stretch generated measurable movements of the index finger. These 'real' movements (mean $= 0{\cdot}20 \pm 0{\cdot}09$ deg) were measured in four out of six trials in which subjects perceived illusory movements and in ten out of twelve trials in which illusory movements were not perceived. In all cases these 'real' movements were below the movement detection threshold determined for a subject. In two trials illusory movements were reported when actual movements of the MCP joint were absent or immeasurably small ($< 0{\cdot}1$ deg).

DISCUSSION

In this study we tested the hypothesis that ensemble cutaneous inputs from the human hand can produce sensations of joint movement. Cutaneous activity was evoked either by electrical stimulation through arrays of skin electrodes or by stretching of the skin. In the majority of subjects (71 %) movement illusions were evoked by one or other of these stimuli. We also evoked illusory movements of the fingers by muscle vibration. Vibration applied laterally to the tendon, which excites predominantly muscle spindle afferents (Roll, Vedel & Ribot, 1989), tended to be more reliable (88 %) and effective in evoking movement illusions than the skin stimulation when all three types of stimulation were applied over their estimated physiological range. The results were therefore consistent with the prevailing view that cutaneous input contributes to human kinaesthesia, but perhaps to a lesser extent than muscle afferent input.

During the preparation of our manuscript, and after our study was complete, Edin & Johansson (1995) published the results of a study in which skin stretch was found to evoke sensations of movement. These investigators were 'unable to elicit movement illusions when skin deformations were applied to a sentient index finger'. This was attributed to the fact that the skin deformations, which were applied by manipulation of the subjects' skin with the experimenters' own fingertips, were accompanied by 'substantial squeezing forces' that the subjects could feel. These sensations apparently masked any underlying joint movement illusions. An ingenious experiment was devised to overcome this problem. Localized skin anaesthesia was used to block the pressure sensations at the points of manipulation, while preserving sensation in adjacent areas of skin being stretched. Illusions of movement were then easy to elicit. Our technique differed from that of Edin & Johansson (1995) in that skin stretch was applied through threads stuck to the skin, avoiding squeezing of underlying tissues and other conflicting sensations. Under these conditions, movement illusions were evoked in the sentient index finger. Furthermore, we were at pains to monitor the small joint movements produced by skin stretching and to compare these with joint movement thresholds for conscious perception. In experiment 3, we verified that real joint movements were below perceptual threshold ($0{\cdot}41 \pm 0{\cdot}13$ deg) when bidirectional, balanced stretches were applied to the skin, the hand being stabilized by suspending all the fingers from a static frame. Our study provides verification that cutaneous sensory activity, rather than the accompanying joint movements or pressure on deep tissues, can be shown to be responsible for sensations of movement in this type of experiment. The conclusion is strengthened by the demonstration of kinaesthetic illusions with electrical stimulation of ensembles of skin afferents.

Electrical stimulation, experiments 1 and 2. The notion of electrically stimulating cutaneous afferents through an array of small surface electrodes arose from a computer animation of strain patterns across the dorsal surface of the hand during individual finger movements (B. B. Edin, personal communication). We reasoned that if skin afferents contributed to kinaesthesia, it should be possible to evoke illusions of movement by independently stimulating groups of them electrically to mimic their ensemble firing patterns. The stimulation we used was highly localized and too weak to activate either joint afferents (which are mostly high-threshold nerve fibres located away from the chosen stimulation sites) or muscle afferents or efferents (as indicated by the higher stimulus strengths required to elicit visible muscle contractions). Illusions of movement were indeed evoked by electrical stimulation in experiments 1 and 2, but only in six out of seventeen subjects (35%). If the three subjects who felt 'as though their fingers should be moving' but knew that they were not (S9, S13 and S16) are included as experiencing movement-related illusions, the overall success rate was still only nine out of seventeen (53%), significantly below that of muscle vibration (88%).

The electrical pulse trains were delivered over three frequency ranges and in two spatial patterns intended to mimic flexion of all the fingers *versus* flexion of the index finger alone. There were cases in which illusory finger movements conformed to the spatial and temporal parameters of the stimuli. However, in several subjects the perceived finger movements were always essentially the same, regardless of the frequency range or spatial pattern of electrical stimulation applied.

An inherent disadvantage of the electrical stimulation technique is that it is not specific to receptors excited by finger movements. Our subjects often reported tactile sensations including scratching, touch, flutter and pressure, all of which are remarkably similar to the sensations described by subjects during microstimulation of single cutaneous afferents (Torebjörk *et al.* 1987). These different and in some cases conflicting sensations may have masked illusions of movement in some of our subjects. If stimulus pulse parameters or patterns could be found that selectively activated the 'right' skin receptors, this might evoke more reliable and graded kinaesthetic illusions.

Skin stretch, experiments 1, 2 and 3. Skin stretch produced illusions of movement in eleven out of nineteen subjects (58%). The spatial pattern of skin stretch more clearly influenced the illusory movements than was the case with electrical stimulation (see Fig. 5). Skin stretch adjacent to the index finger tended to produce illusory movements localized to that finger; stretch adjacent to other fingers generally produced illusory movements in those fingers. In some subjects the amplitude of skin stretch was also reflected in the amplitude of the illusory movements. However, this effect was not statistically significant when tested across subjects. This may be due to differences in optimal stimulus intensities between subjects or to the small sample size in experiment 3. Initially we applied the skin stretch manually (experiments 1 and 2), but we found that it occasionally caused small accompanying joint rotation. Experiment 3 was therefore conducted to validate the findings of experiments 1 and 2. In all cases in which illusory movements were reported in experiment 3, 'real' movements of the fingers were below perceptual threshold or were undetectable ($< 0{\cdot}1$ deg at the MCP joint). An unexpected outcome was that in seven out of eleven subjects skin stretch evoked illusions of movement in the opposite direction to that predicted (i.e. stretching the dorsal skin over the MCP joint caused perceptions of extension, whereas in 'real' movements this area of skin stretches during flexion). We offer four possible explanations for this. (1) Close inspection of the videotaped sessions in experiments 1 and 2 revealed that there may have been small 'real' extension movements in some of the trials. Though reported illusory movements were always of a much larger magnitude than any of these observed 'real' movements, perception of the latter via muscle and joint receptors may have been 'amplified' by cutaneous facilitation (Hulliger *et al.* 1979; Burke *et al.* 1988). However, this explanation seems unlikely in light of the very large difference between the illusory movements evoked in experiment 3 and the accompanying 'real' movements, which were either below detection threshold or undetectable. (2) Similarly, we noticed in the 'real' movement matching trials of experiment 3, when movements were close to perceptual threshold, some subjects detected movement but were unreliable in matching direction, as has been reported previously (Hall & McCloskey, 1983). The incorrect assignment of direction in skin stretch trials, especially those in which illusory movements were very small, may therefore reflect this low threshold of detection and higher threshold for directional resolution. (3) Our technique of stretching the skin over the MCP joint via threads stuck to the skin produced local compression or bunching of the skin close to the attachment points, along the line of pull. Responses of skin receptors in this locally distorted area may provide enough conflicting input to contaminate illusions evoked by the stretched portion of skin (as pointed out by Edin & Johansson, 1995). (4) Finally, our skin stretch stimulation elicited input from only a limited area of the dorsum of the hand, especially in experiment 3. A more physiological stimulus that would include the palmar glabrous skin and a larger area of dorsal hairy skin might have improved directional resolution. The palmar glabrous skin was included in the study of Edin & Johansson (1995) and may account for the higher success rate (5/5 subjects perceived movement) and less ambiguous directional perceptions (all movements were in the hypothesized direction) in that study. Explanations 3 and 4 also suggest that in our study we may have underestimated the potency of skin-evoked kinaesthetic input, particularly when compared with that evoked by vibration. It should be noted that in the ten subjects in whom illusory movements were evoked by both skin stimulation and vibration, the size of the illusions was as follows: larger for skin input in three subjects; larger for muscle input in two subjects; and not significantly different in the other two. This suggests that when skin input does take part in kinaesthesia, it may be just as effective as muscle input.

In experiments 2 and 3 the skin stretch was applied at three different amplitudes to mimic skin stretch amplitudes generated by small, medium and large flexions of the MCP joint. The actual applied skin strain over the MCP joint, averaged across all subjects in experiment 3, ranged from 2·2 to 7·7% of unstretched values for the small to large amplitude stretches, respectively. Edin (1992) reported that the maximal skin strain measured 2–3 cm proximal to the MCP joint during rotation of that joint from fully extended to fully flexed is 10–15%. The firing of slowly adapting types I and II receptors begins to saturate above approximately 10% skin strain (Edin, 1992).

Vibration, experiment 1 and 2. ANOVA revealed that vibration was significantly more effective at evoking illusory movements than electrical stimulation or skin stretch (see Fig. 3). Also, the illusory movements were more consistent within and between subjects. At face value, this supports the view that muscle spindles produce more powerful kinaesthetic effects than cutaneous receptors. However, there are some problems in drawing physiological conclusions from the relative efficacy of the three stimulus modalities in our study. The first and most obvious difficulty is alluded to above. None of the artificial stimuli could have produced completely 'natural' firing patterns in the targeted sensory afferents. Thus although the electrical, stretch and vibratory stimuli were chosen to activate receptors over their estimated physiological range, the spatial and modality-specific recruitment of receptors and the firing elicited in them could only have been a crude approximation of that in natural movements. Second, it is very difficult to estimate the relative proportion of the 'appropriate' afferents recruited by the artificial stimuli. As mentioned above, the skin stretch, and also the electrical stimulation, were limited to only a portion of the dorsal aspect of the hand. Reciprocal signals from the palmar glabrous skin were not included. Similarly, although the vibration may have excited a good proportion of the index finger extensor spindles, it certainly excited additional receptors as well, notably skin receptors under the probe, and it did not elicit the reciprocal reductions in firing of finger flexor spindles that would normally occur during flexion movements (Al-Falahe *et al.* 1990).

While acknowledging the above problems of interpretation, we were nonetheless struck by the ease with which we could elicit kinaesthetic sensations with vibration and the relative difficulty we had in eliciting comparable kinaesthetic sensations with predominantly skin input, even when this was quite intense. This is certainly consistent with the many indirect pieces of evidence that muscle and joint receptors are more crucial than skin receptors in kinaesthesia and position sense (Refschauge, Chan, Taylor & McCloskey, 1995). In contrast, Edin & Johansson (1995) concluded that skin stretch took precedence over joint rotation, at least in the conscious appreciation of certain manual manipulations of skin and joints, when these elicited conflicting signals from skin and muscle receptors. The problem with these latter results is that local anaesthesia probably abolished input from the joint undergoing 'real' rotation, and muscle receptor input was modulated in an unknown way by these movements and by local pressure on the underlying tendons and ligaments from the experimenters' fingers.

Conclusion

Our study confirms that input to the central nervous system from ensembles of skin receptors contributes to the conscious perception of movement. The data left us with the impression that in the human hand, activity in muscle afferents dominates over skin input in eliciting sensations of movement, but because the adequacy of the stimuli in eliciting firing patterns similar to those associated with 'real' joint movement may have varied from one technique to another and for other reasons discussed above, this issue remains open. Similarly, care should be taken in extending these results to kinaesthesia at other joints of the body: skin receptors in the forearm, and indeed, in most of the hairy skin in the rest of the body, may differ substantially from those of the dorsum of the hand (Vallbo, Olausson, Wessberg & Kakuda, 1995). Further study is therefore required to elucidate the kinaesthetic role of cutaneous input at other joints in the body and the relative importance and interactions of the different sensory modalities in kinaesthesia.

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