

# Cutaneous Receptors Contribute to Kinesthesia at the Index Finger, Elbow, and Knee

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Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *J Neurophysiol* 94: 1699–1706, 2005. First published May 25, 2005; 10.1152/jn.00191.2005. The neural mechanisms underlying the sense of joint position and movement remain controversial. While cutaneous receptors are known to contribute to kinesthesia for the fingers, the present experiments test the hypothesis that they contribute at other major joints. Illusory movements were evoked at the interphalangeal (IP) joints of the index finger, the elbow, and the knee by stimulation of populations of cutaneous and muscle spindle receptors, both separately and together. Subjects matched perceived movements with voluntary movements of homologous joints on the contralateral side. Cutaneous receptors were activated by stretch of the skin (using 2 intensities of stretch) and vibration activated muscle spindle receptors. Stimuli were designed to activate receptors that discharge during joint flexion. For the index finger, vibration was applied over the extensor tendons on the dorsum of the hand, to evoke illusory metacarpophalangeal (MCP) joint flexion, and skin stretch was delivered around the IP joints. The strong skin stretch evoked the illusion of flexion of the proximal IP joint in 6/8 subjects ( $12 \pm 5^\circ$ , mean  $\pm$  SE). For the group, strong skin stretch delivered during vibration increased the perceived flexion of the proximal IP joint by eight times with a concomitant decrease in perceived flexion of the MCP joint compared with vibration alone ( $P < 0.05$ ). For the elbow, vibration was applied over the distal tendon of triceps brachii and skin stretch over the dorsal forearm. When delivered alone, strong skin stretch evoked illusory elbow flexion in 5/10 subjects ( $9 \pm 4^\circ$ ). Simultaneous strong skin stretch and vibration increased the illusory elbow flexion for the group by 1.5 times compared with vibration ( $P < 0.05$ ). For the knee, vibration was applied over the patellar tendon and skin stretch over the thigh. Skin stretch alone evoked illusory knee flexion in 3/10 subjects ( $8 \pm 4^\circ$ ) and when delivered during vibration, perceived knee flexion increased for the group by 1.4 times compared with vibration ( $P < 0.05$ ). Hence inputs from cutaneous receptors, muscle receptors, and combined inputs from both receptors likely subserve kinesthesia at joints throughout the body.

## INTRODUCTION

Kinesthesia, the sense of position and movement, is a vital component of proprioception, and its disturbance markedly impairs voluntary movement (e.g., Cole 1995; Rothwell et al. 1982). However, understanding the mechanisms that mediate this ability has long been controversial (for review, see McCloskey 1978). For more than 100 years, opinion swayed between an important role for central signals associated with

the command to move (Helmholtz 1867; von Holst 1954) and peripheral feedback from sensory receptors (Sherrington 1900). During the latter half of the 20th century, the balance tipped toward a peripheral origin, at least for perception of limb movements, and the focus then shifted to identification of which sensory receptor predominated. Arguments for receptors located in muscle (Goodwin et al. 1972; Matthews 1977; McCloskey et al. 1983), joints (Boyd and Roberts 1953; Ferrell et al. 1987; Gelfand and Carter 1967), and the skin (Edin and Abbs 1991; Gandevia and McCloskey 1976; Provins 1958) have been advanced, but during the last 30 years, a consensus has developed that feedback from muscle spindle receptors is the most important source of proprioceptive information (e.g., Gandevia 1996; Kandel et al. 2000; Smetacek and Mechsner 2004). This idea stemmed originally from the finding of powerful illusions of position and movement when muscle spindles were activated by tendon vibration (Goodwin et al. 1972) but has been corroborated using a variety of methods (e.g., Gandevia 1985; Gandevia and McCloskey 1976; McCloskey et al. 1983). Despite this, proponents for a role for cutaneous receptors remained, initially based on clinical observations during reconstructive surgery (Moberg 1972, 1983) but also from experiments in which cutaneous feedback was removed by anesthesia (e.g., Gandevia and McCloskey 1976; Moberg 1983; Refshauge et al. 2003). Subsequent microneurographic studies lent support to a potential cutaneous contribution to kinesthesia; cutaneous receptors in the hand (Edin 1992, 2004; Edin and Abbs 1991; Grill and Hallett 1995; see also Burke et al. 1988; Hulliger et al. 1979) and around the knee (Edin 2001) can provide information about the position and movement of nearby joints. Although joint receptors probably contribute (Ferrell et al. 1987), this has been difficult to demonstrate and the lack of a major proprioceptive deficit on removal of joint receptor feedback has contributed to the diminishing attention they receive.

Just as the signaling of arterial pressure by baroreceptors does not mean that arterial pressure must be perceived, the fact that cutaneous receptors provide adequate signals of joint movement does not ensure that the CNS uses this afferent signal for sensation of joint movement. Two groups assessed whether cutaneous receptors contribute to the perception of movements of the fingers (Collins and Prochazka 1996; Edin and Johansson 1995). Both found that stimulation of cutaneous receptors of the hand produced illusions of finger movement.

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This provided the first evidence that cutaneous receptors contribute directly to kinesthesia. Whether cutaneous receptors generate illusory movements at joints other than the fingers has not been tested. Theoretically, cutaneous feedback may not be as important at more proximal joints as they are crossed by uniaxial muscles from which resident muscle spindles may provide unambiguous information for accurate movement perception (Verschueren et al. 1998). Furthermore, removal of cutaneous feedback by anesthesia of the skin around the fingers (e.g., Gandevia and McCloskey 1976; Provins 1958; Refshauge et al. 1998), but not the knee (Clark et al. 1979), markedly impaired movement detection. However, cutaneous receptors over a wide area of the leg provide accurate information about knee movement (Edin 2001), and it has been argued that the lack of an effect at the knee (Clark et al. 1979) may reflect the small area of cutaneous anesthesia (Edin 2001).

The present experiments address two questions. First, do cutaneous receptors contribute to position and movement sense at limb joints throughout the body? To test this, cutaneous receptors were activated to evoke illusions of movement at three joints. The index finger interphalangeal (IP) joints were chosen because a previous study has demonstrated a role for cutaneous feedback in kinesthesia at the proximal IP joint (Edin and Johansson 1995), but the illusory movements were not quantified. In addition, comparative data exist for the metacarpophalangeal (MCP) joints (Collins and Prochazka 1996; Collins et al. 2000). The elbow and knee were chosen to test, for the first time, whether cutaneous receptors contribute to kinesthesia at larger and more proximal joints. Second, does the CNS use feedback from cutaneous and muscle spindle receptors simultaneously at these joints? To test this, we compared the amplitude of illusory movements produced by the activation of muscle spindle and cutaneous receptors separately and together for each joint. We hypothesized that each afferent modality would evoke illusory movements when activated separately and when activated together, movement illusions would reflect the combined afferent volley. A brief report of some data has been presented (Collins et al. 2001).

## METHODS

Fourteen subjects between the ages of 23 and 43 yr participated. All were volunteers and participated in accordance with the Declaration of Helsinki. Subjects had no history of neuromuscular disease. Eleven of the 14 subjects were naive to the research hypothesis and one author participated. All procedures were approved by the local Human Research Ethics Committee.

In a given session, movement illusions were studied at the index finger, elbow, or knee. Each session lasted ~2 h. Some subjects participated in more than one session. For all testing, subjects were seated and all stimuli were applied on the right side. The "test" limb was held firmly in place to prevent movement during the stimulation. Muscle spindles were activated by vibration, and cutaneous receptors were activated by manual stretching of the skin. Both stimuli were designed to activate receptors that discharge during passive joint flexion. The vibration and skin stretch were delivered separately and together. Subjects were informed that the experiments were designed to investigate how humans interpret feedback from sensory receptors and that some trials may include movement. If they detected movement, they were to match it with a simultaneous movement of the homologous joint(s) on the contralateral (left) side. A barrier prevented subjects from seeing the experimental manipulations on the

right side, and thus they remained unaware that the test joint was never actually moved.

## Stimuli

**VIBRATION.** Vibration at 100 Hz (~1 mm, Wahl, No. 4013) was applied over the finger extensor tendons to evoke the illusion of flexion of the test joint (Fig. 1). When consistent movement illusions were evoked the vibrator was secured with a clamp attached to a nearby table.

**SKIN STRETCH.** Figure 1 shows the method used to manually stretch the skin around each joint. Fine threads were attached to the skin with pieces of adhesive tape. These threads were attached to elastic bands, and the skin was stretched and relaxed cyclically (see following text). The stretch was delivered at two intensities (weak and strong) to mimic skin strain during small and large joint flexion movements. The skin stretch was similar to that used previously (Collins and

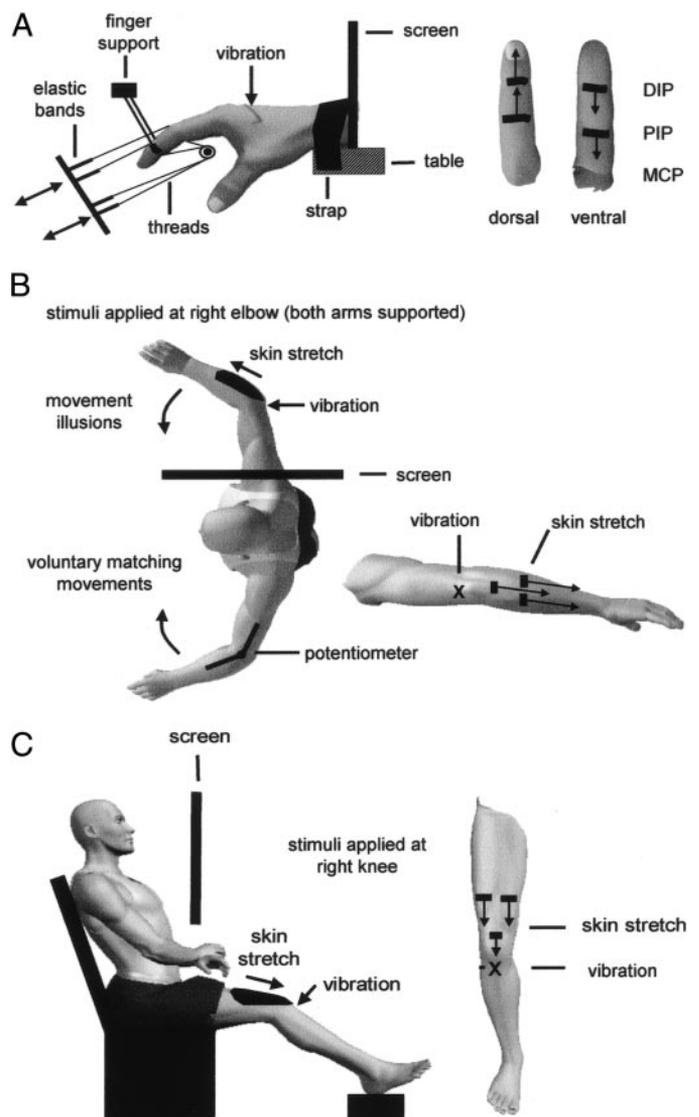


FIG. 1. Diagram of the experimental setup. *A*: the application of the skin stretch to the right index finger (DIP, distal interphalangeal joint; PIP, proximal interphalangeal joint; MCP, metacarpophalangeal joint). *B* and *C*: the skin stretch application for the right elbow and knee, respectively. Perceived movements were matched with voluntary movements of the homologous joint(s) on the contralateral side.

Prochazka 1996; Collins et al. 2000) and has been calculated to result in 2–8% skin strain (Collins and Prochazka 1996). The timing and amplitude of the stretch was monitored using a strain gauge attached in series with the elastic bands.

### Protocol

Stimuli were delivered in five ways: vibration alone, weak skin stretch alone, strong skin stretch alone, vibration *and* weak stretch, and vibration *and* strong stretch. All stimuli were delivered cyclically. For one cycle of stimulation, the stimuli were on for 2–4 s and off for an equivalent time (2–4 s). The cycle duration was adjusted for each subject to obtain the most reliable illusion of movement. This duration was identified at the beginning of each session and then was not changed. When delivered together, the skin stimuli and vibration were delivered in-phase (i.e., both on and both off at the same time). Prior to data collection, subjects were provided with several cycles of one type of stimulation (~5–20 cycles) until they reported that they were matching accurately the perceived movements. They then received a set of five consecutive cycles of each stimulation during which the matching movements were recorded. This slight variation from procedures used in our previous study (Collins et al. 2000) reduced the cycle-to-cycle variability in matching movements and increased the ability to detect differences for individual subjects in illusory movements evoked by the different types of stimuli. In the present study, subjects could use vision to guide the matching movement and confirmed that they were matching accurately the movements perceived during data collection. For each subject, data were recorded during 15 cycles of vibration alone (i.e., 3 sets of 5), 10 cycles of weak skin stretch, 10 cycles of strong skin stretch, 10 cycles of vibration *and* weak skin stretch, and 10 cycles of vibration *and* strong skin stretch. The order of the different stimuli was randomized across subjects.

**INDEX FINGER.** Eight subjects participated. They were seated with both arms resting on a table in front of them. The right arm was strapped down and supported up to the wrist (Fig. 1A). A rigid support attached to the lateral sides of the distal IP joint of the index finger held the finger in a slightly flexed position (all joints  $\sim 10^\circ \pm$ ) and prevented movement during the experiment. The other fingers were held in a similar position with adhesive tape. The left arm rested on the table but was otherwise free to move. Vibration was applied to the dorsum of the hand over the tendons of the extensor indicis and extensor digitorum communis muscles  $\sim 2$  cm proximal to the index finger MCP joint as described by Collins and Prochazka (1996). The vibration was adjusted to evoke a consistent illusion of flexion at the MCP joint. The skin stretch was applied to the dorsal and ventral sides of each IP joint to simulate skin stretch during normal flexion movements (Fig. 1A). On the dorsum, strings taped  $\sim 3$ – $5$  mm distal to the center of each joint, were pulled in a distal direction, stretching the skin directly over each joint. On the ventral side, threads were taped  $\sim 1$  mm proximal to the crease under each IP joint. These were pulled in a proximal direction to compress the ventral skin.

**ELBOW.** Ten subjects participated. They were seated in a semi-reclined position with both arms supported at shoulder height and the elbows flexed  $\sim 30^\circ$  (Fig. 1B). The right arm was secured to prevent movement and the left arm rested on a table but was free to move. Vibration was applied over the tendon of the triceps brachii just proximal to the ulnar head. Skin stretch was delivered through two to four pieces of adhesive tape applied to the skin  $\sim 4$ – $8$  cm distal to the elbow.

**KNEE.** Ten subjects participated. They were seated in a semi-reclined position with knees flexed  $\sim 45^\circ$  and heels resting on a support (see Fig. 1C). Vibration was applied over the patellar tendon. The skin stretch was applied to the anterior thigh.

### Data collection and analysis

The matching movements were recorded using potentiometers placed over the axis of rotation of the matching joint(s) on the left side of the body. For index finger movements, the potentiometers were placed across the MCP and proximal IP joints. Signals of movement were digitized (50 Hz) and stored for subsequent analysis along with signals for the timing of the stimuli. The peak-to-peak amplitude of each matching movement was measured with a resolution of  $<0.1^\circ$ , and mean movement amplitudes were calculated separately for cycles of vibration alone and skin stretch alone and when both stimuli were applied together. Flexion movements were assigned a positive value and extension movements a negative value. If no movement was recorded, a value of zero was assigned.

Statistical analyses were performed to assess the influence of skin stretch on movement perception for individual subjects and for the group. Tests for differences from when vibration was delivered alone were performed using one-way ANOVAs on data from individual subjects and group data were analyzed using one-way repeated-measures ANOVA on the mean data from individual subjects. When significant differences were identified, post hoc analyses were conducted using Fisher LSD tests. Mann-Whitney *U* tests were used to identify whether illusions produced when the skin stretch was delivered alone were statistically significant for individual subjects by testing whether perceived movement amplitudes were significantly different from zero. For all tests, statistical significance was accepted when  $P < 0.05$ . Descriptive statistics are reported as the means  $\pm$  SE.

## RESULTS

Alone or in combination, stimulation of muscle spindle endings by vibration and cutaneous receptors by skin stretch evoked illusory movement at the index finger, elbow, and knee. Perceived movements were assessed from the magnitude of voluntary “matching” movements of homologous joints on the contralateral side.

### Index finger

Vibration over extensor tendons on the dorsum of the hand evoked illusory flexion of the index finger. Cutaneous receptors were activated around both IP joints by stretching the skin. Matching movements with the contralateral MCP and proximal IP joints were recorded, and the following quantitative description of the illusory movements will be restricted to these joints. However, matching movements performed with the distal IP joint were of a similar amplitude and direction to those recorded for the proximal IP joint (see DISCUSSION).

Figure 2 shows data for one subject in whom illusory flexion movements were perceived primarily at the MCP joint during vibration and at the IP joints during skin stretch. The same format is used for Figs. 4 and 6. Figure 2A shows the timing of stimuli delivered to the right index finger and the matching voluntary movements of the contralateral finger during “sets” of five cycles of stimulation. The mean amplitude of the perceived movements for all trials for this subject is shown in B. Compared with vibration only, combined skin stretch and vibration increased significantly the illusory flexion of the proximal IP joint and significantly reduced it for the MCP joint. Figure 2C shows the actual position of the finger in light gray and in darker gray the mean amplitude of the perceived movements during vibration (*top*) and combined vibration and strong skin stretch (*bottom*).

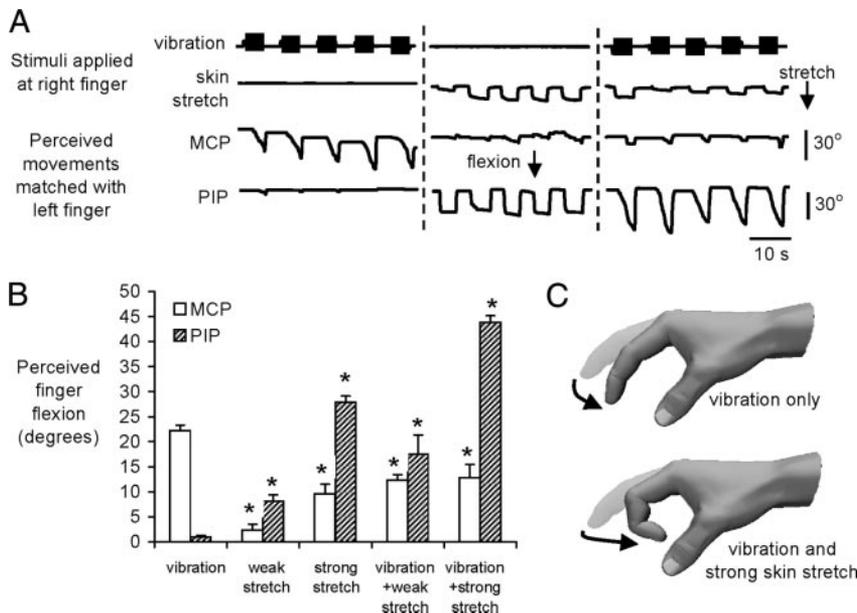


FIG. 2. Data from 1 subject for trials in which vibration and skin stretch were applied at the right index finger. *A*: the timing of the delivery for the different types of stimulation and the recording from the potentiometers over the MCP and proximal IP joints of the contralateral hand while the subject matched perceived movements of the right index finger. *B*: the mean amplitude of the perceived index finger movements at the MCP and proximal IP joints for all trials (vibration  $n = 15$  cycles, all others  $n = 10$  cycles). \*, significant differences in perceived amplitude of movement from vibration alone. The diagrammatic images in *C* show the position of the right index finger during the experiment (gray silhouette) and the average perceived finger position when vibration alone was applied (*top*) and simultaneously with skin stretch at the IP joints (*bottom*). For *C*, the distal IP joint angles were estimated.

Mean data for the group of eight subjects are shown in Fig. 3. There was a significant main effect for type of stimulation at both the MCP [ $F(4,28) = 8.3, P < 0.001$ ] and proximal IP joints [ $F(4,28) = 6.8, P < 0.001$ ]. When delivered alone, both intensities of skin stretch evoked illusions of movement that were statistically significant in 6/8 subjects. These were always of IP flexion (joint underlying the region of stretched skin) and typically involved small movements perceived at the MCP

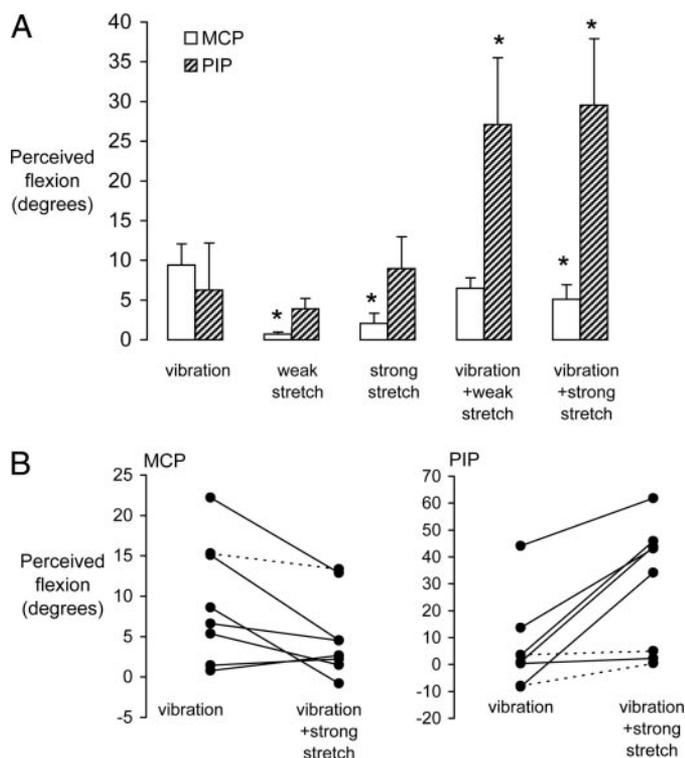


FIG. 3. Illusory movements at the MCP and proximal IP joints for the group ( $n = 8$ ). *A*: the mean amplitude of illusory movements evoked by each type of stimulation. \*, significant differences from the vibration-only trials for each joint. *B*: the amplitude of the movements perceived by each subject during periods of vibration compared with those during simultaneous vibration and strong skin stretch. —, data connected that are significantly different.

joints as well. When the skin stretch and vibration were applied simultaneously, subjects perceived significantly more flexion at the proximal IP joint during both weak and strong stretch compared with when vibration was applied alone (Fig. 3*A*). The increase was approximately four and eight times for the weak and strong stretch, respectively. The combined vibration and strong skin stretch resulted in significantly less flexion perceived at the MCP joint than vibration alone. The mean amplitude of illusory movements produced by vibration alone and by combined vibration and strong skin stretch are shown for each subject in Fig. 3*B*. During simultaneous vibration and strong stretch, perceived proximal IP flexion significantly increased in 6/8 subjects compared with vibration only, and MCP flexion significantly decreased in 7/8 subjects. During simultaneous vibration and weak stretch, perceived proximal IP flexion significantly increased in all eight subjects and perceived MCP flexion decreased in 4/8 subjects, compared with vibration only.

#### Elbow

Vibration was applied over the distal tendon of triceps brachii and regions of skin were stretched over the dorsal aspect of the forearm. Figure 4 shows data from one subject for whom both types of stimulation evoked the illusion of elbow flexion when delivered separately and their amplitudes were similar. Movements perceived during combined stimulation were significantly larger than during the vibration alone for both intensities of skin stretch. Further, the size of the elbow flexion illusion was significantly greater when vibration was combined with the strong stretch compared with the weak stretch.

Mean data for the group of 10 subjects are shown in Fig. 5. The weak and strong skin stretch evoked a significant illusion of elbow flexion in 4/10 subjects and 5/10 subjects, respectively. There was a significant effect of stimulation type [ $F(4,36) = 14.0, P < 0.001$ ]. Skin stretch alone resulted in significantly less perceived elbow flexion than when vibration was delivered alone. When vibration and skin stretch were

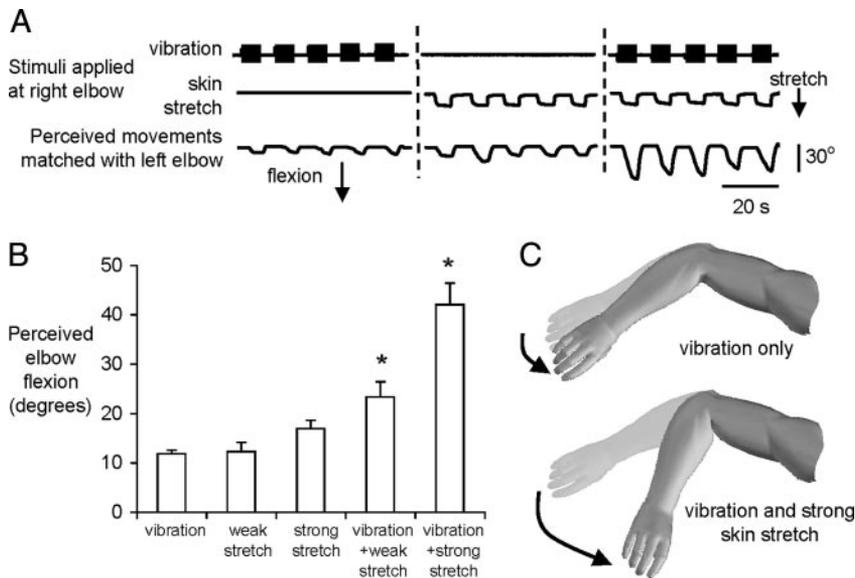


FIG. 4. Data from 1 subject for trials in which vibration and skin stretch were applied at the right elbow. *A*: the timing of stimulus delivery and movements recorded at the left elbow while the subject matched perceived movements of the right elbow. *B*: the mean amplitude of the perceived movements for all trials (vibration  $n = 15$  cycles, all others  $n = 10$  cycles). \*, significant differences in illusory movement amplitudes from vibration alone. The diagrammatic images in *C* show the position of the right elbow during the experiment (gray silhouette) and the average perceived position when vibration was applied by itself (*top*) and simultaneously with strong skin stretch near the elbow (*bottom*).

delivered together, perceived elbow flexion was 1.3 (weak stretch) and 1.5 times larger (strong stretch) than that when the vibration was applied alone. This increase was significant for the strong skin stretch only. The mean amplitude of illusory movements produced by vibration alone and by combined vibration and strong skin stretch are shown for each subject in Fig. 5*B*. Simultaneous vibration and strong stretch increased significantly the illusion of elbow flexion in 6/10 subjects. With weak skin stretch the illusion increased significantly in 5/10 subjects and decreased in one.

*Knee*

Vibration was applied over the patellar tendon and regions of skin were stretched over the dorsal aspect of the thigh. Data from one subject in whom both types of stimulation evoked the illusion of knee flexion when delivered separately are shown in Fig. 6. When skin stretch was applied alone, the illusory flexion was significantly greater during the strong stretch than the weak stretch. During vibration, skin stretch increased the size of the illusory knee flexion significantly, compared with vibration alone, but there was no significant difference between the effects of the two strengths of skin stretch.

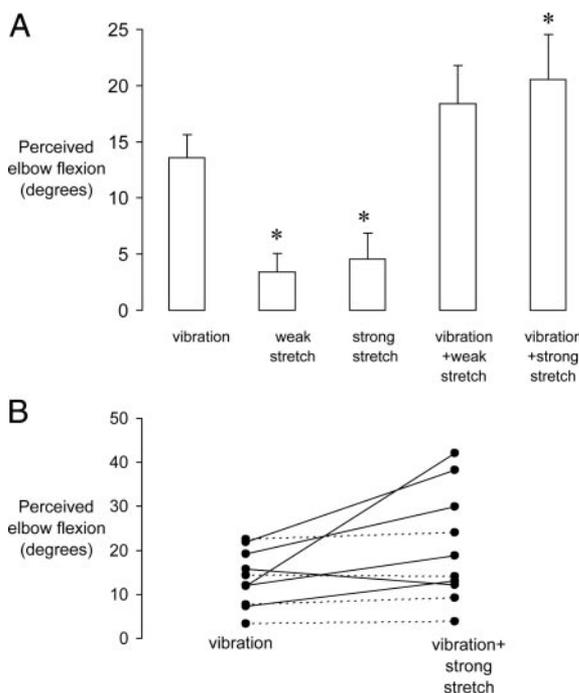


FIG. 5. Illusory movements at the elbow for the group of subjects ( $n = 10$ ). *A*: the mean amplitude of the movements perceived at the elbow during each type of stimulation. \*, significant differences from the vibration only trials. *B*: the amplitude of illusory movements perceived by each subject during periods of vibration compared with those during simultaneous vibration and strong skin stretch. —, data connected that are significantly different.

Mean data for the group of 10 subjects are shown in Fig. 7. There was a significant effect of stimulation type [ $F(4,36) = 16.7, P < 0.001$ ]. Both weak and strong skin stretch when delivered alone evoked a significant illusion of knee flexion in 3/10 subjects, and the skin stretch produced a significantly smaller illusion of knee flexion than when vibration was delivered alone for both intensities of skin stretch. Delivered together, vibration and strong skin stretch resulted in illusory movements that were 1.4 times larger than when the vibration was applied alone, and this effect was significant. Figure 7*B* shows the mean amplitude of perceived movements during vibration compared with simultaneous vibration and strong skin stretch for each subject. Simultaneous vibration and weak stretch increased significantly the illusion of knee flexion in 3/10 subjects but decreased it in 5/10. Simultaneous vibration and strong stretch also altered the illusion of knee flexion in 8/10 subjects, significantly increasing it in 5/10 subjects and decreasing it in 3/10.

DISCUSSION

These experiments show that activation of cutaneous receptors can evoke illusory movements of the index finger, elbow, and knee. This is the first direct evidence to support the hypothesis that cutaneous receptors can generate proprioceptive sensation at joints other than those of the hand. When cutaneous and muscle spindle receptors at these joints were activated simultaneously, movement illusions usually increased above those produced by tendon vibration alone and

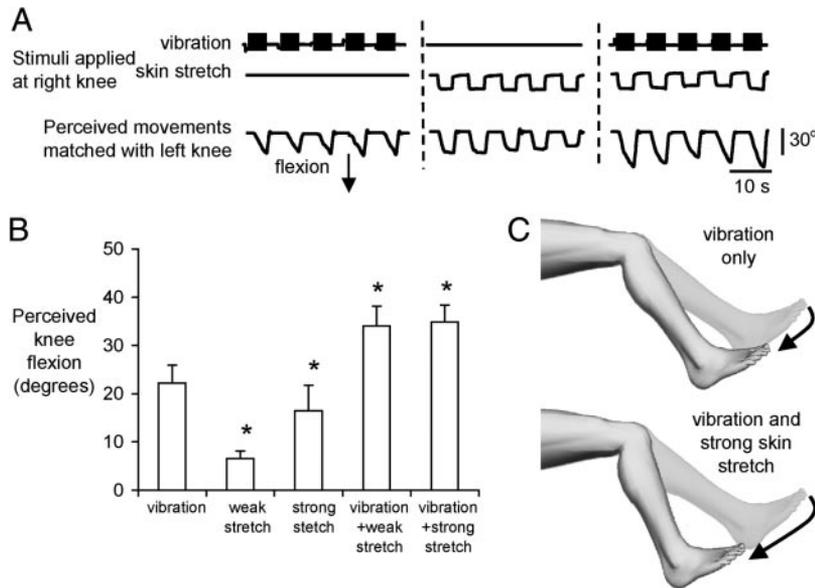


FIG. 6. Data from 1 subject for trials in which vibration and skin stretch were applied at the right knee. *A*: the timing of the different stimuli and movements recorded at the left knee while the subject matched illusory movements of the right knee. *B*: the mean amplitude of the perceived movements for all trials (vibration  $n = 15$  cycles, all others  $n = 10$  cycles). \*, significant differences in illusory movement amplitudes from vibration alone. The diagrammatic images in *C* show the position of the right knee during the experiment (gray silhouette) and the average perceived position when vibration was applied by itself (dark gray; *top*) and simultaneously with strong skin stretch near the knee (dark gray; *bottom*).

thus they are likely to reflect the central combination of both inputs.

#### Movement illusions evoked by activation of cutaneous receptors

Previously, the cutaneous contribution to kinesthesia had only been tested directly for joints of the fingers (Collins and Prochazka 1996; Collins et al. 2000; Edin and Johansson 1995). Here, we activated selectively cutaneous receptors in regions of skin that are stretched during flexion of the index

finger IP joints, the elbow, and the knee to try to evoke illusions of movement, about the stationary “test” joint, consistent with the evoked cutaneous volleys. Manual stretching of the skin around the stationary test joint generated illusory movements that varied in amplitude, but were as large as 28° at the proximal IP joint, 45° at the elbow, and 16° at the knee. In some subjects, perceived movements were small or no movement was perceived. Such variability is similar to data previously obtained for the finger joints (Collins and Prochazka 1996). This may reflect differences in the effectiveness of the stimuli to mimic a movement-related cutaneous signal or individual differences in interpretation of the artificial sensory signals. In addition, individuals may differ in the extent to which they use cutaneous input for kinesthesia.

As the current method for applying skin stretch cannot replicate the complex skin strain *patterns* that occur during natural movements, our results may underestimate the importance of cutaneous feedback for kinesthesia (see also following text). Nonetheless, skin stretch alone evoked significant illusions of movement 48% of the time (27/56 cases). The *amplitude* of the presently applied skin stretch was similar to that used previously (Collins and Prochazka 1996; Collins et al. 2000) and calculated to be ~2–8% skin strain (Collins and Prochazka 1996). This is comparable to that during normal finger movements (Edin 1992). The *rate* at which the stretch was applied probably mimicked discharge during relatively slow movements and was less than that used by Edin (1992, 2004) to quantify the dynamic sensitivity of cutaneous receptors. The “slow” skin stretch in the present study may also contribute to underestimate the cutaneous contribution to kinesthesia. In contrast, vibration may generate muscle spindle firing rates much higher than those during natural movements, perhaps leading to an overestimation of their proprioceptive importance (Edin 2001).

During all experiments, the test joint was fixed so that activation of noncutaneous receptors by actual movements of the test joint was unlikely (see also Collins and Prochazka 1996). Hence, illusions evoked by skin stretch alone occurred despite “conflicting” signals from muscle spindles signifying a

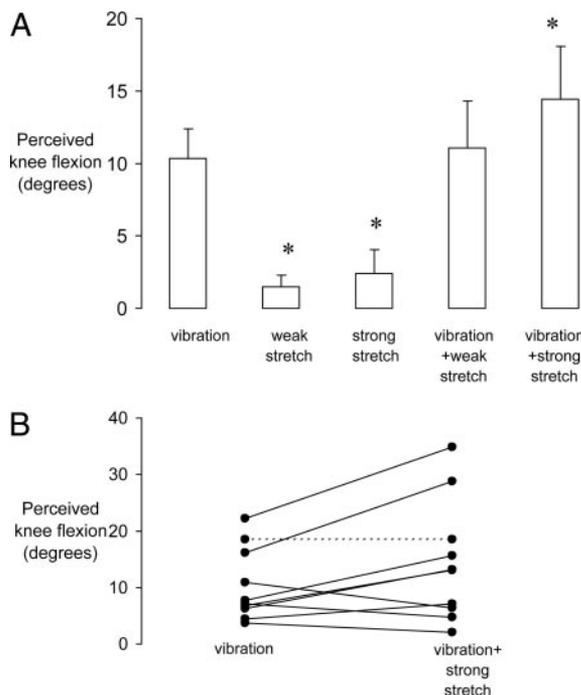


FIG. 7. Illusory movements at the knee for the group of subjects ( $n = 10$ ). *A*: the mean amplitude of the movements perceived at the knee during each type of stimulation. \*, significant differences from the vibration only trials. *B*: the amplitude of illusory movements perceived by each subject during periods of vibration compared with those during simultaneous vibration and strong skin stretch. —, data connected that are significantly different.

stationary joint. This might indicate that feedback from cutaneous receptors takes precedence over that from muscle spindles for kinesthesia (Edin 1995). An alternative possibility, and one that we favor, is that the CNS uses information from the afferent channel or channels that are changing as in other sensory systems. Accordingly, movement illusions are also perceived during tendon vibration when the skin is anesthetized (Goodwin et al. 1972). For assessment of movement illusions at the index finger, the "matching" movements were constrained by anatomical and physiological limitations to perform independent movements of the IP joints (e.g., Kilbreath and Gandevia 1994; Zatsiorsky et al. 2000). This could have restricted the subjects' ability to match accurately the perceived movements. Also illusory movements can reach positions that are not possible to achieve voluntarily (Craske 1977; Gandevia 1985). However, our subjects could use vision to guide the matching movements and were satisfied with their matching accuracy, and thus our measure of the illusions of movement was unlikely to be limited in a major way by constraints on the voluntary matching movements.

It has been argued that cutaneous feedback might be more important for kinesthesia at the fingers than at more proximal joints (Clark et al. 1979; Collins et al. 2000; Moberg 1983; Verschuere et al. 1998). Anesthesia of the skin around the fingers (Gandevia and McCloskey 1976; Provins 1958; Refshauge et al. 1998) but not the knee (Clark et al. 1979) reduced movement perception. Also the fingers, particularly the index finger, are controlled by many multiarticular muscles. The discharge of muscle spindle endings (Grill and Hallett 1995; Verschuere et al. 1998) and some types of cutaneous receptors (Edin 1991) does not unambiguously encode movements at a single joint. However, feedback from rapidly adapting cutaneous receptors in the hand may help signify which particular joint has moved (Edin 1992; Edin and Abbs 1991; Grill and Hallett 1995; see following text). Our present and previous results (Collins et al. 2000) suggest that the CNS uses this information to help identify which finger joint is moving. However, cutaneous feedback may be less important at proximal joints where signals from spindles in uniaxial muscles may suffice. The present observation that the cutaneous stimuli evoked movement illusions that were larger and present in more subjects at the fingers than at the elbow or knee would support this notion of a regional difference in the kinesthetic importance of cutaneous receptors. However, the stimuli used for the fingers, which included the dorsal and ventral skin, may have better mimicked movement-related receptor discharge than those for the more proximal joints where only the dorsal skin was stretched. We predict that activation of the skin on both sides of the joint would be more effective at creating illusion of movement at the elbow and knee (see Collins et al. 2000). Thus the present results demonstrate that cutaneous receptors contribute to kinesthesia at proximal and distal joints, but the relative importance of this contribution for each joint is still unclear. Indeed, cutaneous receptors over a large area of the thigh can provide signals related to knee movement with a dynamic sensitivity almost an order of magnitude greater than the sensitivity of cutaneous receptors in the hand for finger movements (Edin 2001).

### *Kinesthetic integration of feedback from cutaneous and muscle spindle receptors*

Does the CNS use feedback from cutaneous and muscle spindle receptors simultaneously for movement perception? We had shown previously that when vibration was applied on the dorsum of the hand to evoke illusions of flexion of the four MCP joints and the skin over selected MCP joints was stimulated, the illusions "focused" to the joint under the region of skin being stimulated (Collins et al. 2000). Specifically, the magnitude of perceived flexion increased at the joint underlying the skin stimulus, and diminished progressively at the more distant MCP joints. A similar "focusing" effect was observed in the present experiments. When spindle discharge from receptors in the long extensors that cross all three joints of the index finger was combined with stretch of the skin around only the two distal joints, the amount of perceived flexion at the distal joints increased and that at the MCP joint decreased. Thus cutaneous feedback helps identify which finger is moving and which joints within the finger are moving. Likely candidates for this focusing effect are the fast-adapting receptors that are localized near individual joints and respond dynamically to both flexion and extension movements primarily of only one joint (Edin and Abbs 1991).

The magnitude of illusory movements at the elbow and knee also reflected combined feedback from cutaneous and muscle spindle receptors. For the group of subjects, simultaneous strong skin stretch and vibration resulted in greater illusory flexion than vibration alone. The discharge of slowly adapting receptors with large receptive fields is primarily unidirectional, increasing during flexion and decreasing during extension in proportion to the position and velocity of more than one joint (Edin and Abbs 1991). Feedback from these receptors may contribute to the perception of movement velocity and amplitude (Edin 1992; Edin and Abbs 1991; Johnson 2001, 2004) and could account for the dependence of the presently reported movement illusions on the size of the skin stretch for some subjects.

Although externally applied skin stretch will not have duplicated natural skin strain patterns, it was sufficient to alter the vibration-induced movement illusions 77% of the time (43/56 cases). This illustrates the influence of cutaneous feedback on proprioceptive sensation at the three tested joints. In some cases, the vibratory illusions decreased, contrary to our hypothesis, which may be due to conflicting signals arising from the cutaneous receptors due to a poor match of natural cutaneous discharge. The volley initiated by the external vibration is also artificial and will comprise muscle spindle as well as cutaneous inputs (Vallbo et al. 1979). While the resulting movement illusions currently attributed to muscle spindles might seem consistent with stretch of the skin under the vibrating probe, vibration applied over a site off the tendon did not result in the illusion of movement (Goodwin et al. 1972). Nonetheless, vibration-induced illusions may contain a contribution from cutaneous receptors or their noise-enhanced central actions (Collins et al. 1996; Manjarrez et al. 2003). However, the importance of muscle spindles for kinesthesia has been established using a variety of approaches (Gandevia 1985; Gandevia and McCloskey 1976; Goodwin et al. 1972; McCloskey et al. 1983).

Finally, a previous view about the role of cutaneous inputs in kinesthesia should be considered. When anesthesia of the skin around the fingers reduced movement perception, the deficit was suggested to reflect loss of a general facilitation of the noncutaneous proprioceptive inputs (e.g., Gandevia and McCloskey 1976; Provins 1958; Refshauge et al. 1998). Such a facilitatory role for tonic cutaneous input was not supported by the results of recent experiments testing the detection of finger movements when the two adjacent digits were anesthetized (Refshauge et al. 2003). Hence, an emerging view, supported by a combination of psychophysical and microneurographic data (Edin 1992, 2001, 2004; Johnson 2001, 2004) is that cutaneous feedback provides accurate perceptual information about joint position and movement and this is integrated with feedback from muscle spindles to provide judgements of position and movement for joints throughout the body. An implication of the present results is that one should be careful about ascribing a proprioceptive deficit to impairment within one afferent modality. Furthermore, in conducting simple tests of proprioception it is likely that the cutaneous input generated by holding the test joint will affect the outcome.

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