

The detection of human finger movement is not facilitated by input from receptors in adjacent digits

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These experiments were designed to determine whether cutaneous input from a digit provides a general facilitation of the detection of movements applied to an adjacent digit. The ability to detect passive movements at the proximal interphalangeal joint of the right index finger was measured when cutaneous (and joint) input was removed (using local anaesthesia) from the tip of one or both digits adjacent to the test finger (16 subjects). The same parameter was also measured when input was artificially increased by stimulation of the adjacent digits at three intensities: below, above and at perceptual threshold (PT; 15 subjects). Detection of flexion or extension movements was not altered by anaesthesia of one or both adjacent digits. Since it was possible that too few tonically active afferents in the hand had been blocked to reveal an effect, the median nerve was blocked, with movements applied to the little finger, causing no measurable impairment in acuity (three subjects). Simultaneous electrical stimulation of the tips of the adjacent digits at intensities above PT impaired movement detection, but had no effect when delivered at or below PT. To test whether the effect of detectable electrical stimuli was due to a specific interaction between the artificial input and the input evoked by moving the digit, or due to mental distraction, stimuli were delivered above PT to either the left or right little finger, or the test index finger during movement of the index finger. Electrical stimulation of the index finger significantly reduced detection by ~50 %, but stimulation of the remote little fingers did not. Electrical stimulation is a non-natural stimulus, so a 'natural' stimulus was applied by continuously stroking the tips of the adjacent digits with a brush (10 subjects). The natural stimulus also significantly reduced movement detection by ~50 %. Together, these findings suggest that tonic inputs from digital nerve afferents adjacent to, or more remote from the passively moved finger do not facilitate movement detection. However, the reduced detection during stimulation of the adjacent digits shows that there is nevertheless some interaction between the various proprioceptive inputs from the digits.

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It is well established that muscle, joint and cutaneous receptors can contribute to the sensations of limb position and movement. This derives from two key observations. First, these receptors are activated when joints are moved. Secondly, this discharge can influence the perception of limb position and movement, based on psychophysical studies in which the discharge is abolished (for example by anaesthesia) or enhanced artificially (for example by electrical stimulation). The first observation goes back to early recordings of afferent discharge in animals (e.g. Adrian *et al.* 1931) and has been amply established in humans using microneurography for muscle (e.g. Vallbo, 1974; Burke *et al.* 1976; Edin & Vallbo, 1990; Grill & Hallett, 1995), joint (Burke *et al.* 1988; Edin, 1990) and cutaneous afferents (Knibestöl, 1975; Hulliger *et al.* 1979; Edin & Abbs, 1991; Grill & Hallett, 1995). Thus, none of the three inputs should be denied a proprioceptive role on the grounds of a failure to discharge. Despite this, it has

been common for joint (e.g. Merton, 1964) or muscle receptors (e.g. McCloskey, 1978) to be considered the main class of proprioceptive afferent.

The second observation, that sensory discharge affects the perception of limb movement, also has a long history, particularly for the impairment of proprioceptive sensation produced by anaesthesia of the digital nerves (Brown *et al.* 1954; Provins, 1958). Artificial enhancement of the discharge of proprioceptive afferents was exploited to demonstrate a proprioceptive role for muscle receptors that are sensitive to vibration (e.g. Goodwin *et al.* 1972; Roll & Vedel, 1982) or to low-threshold electrical stimulation (Gandevia, 1985). More recently, this approach has been extended. Microstimulation of joint afferents can evoke at least some proprioceptive sensations (Macefield *et al.* 1990), and cutaneous receptors activated by movement of nearby joints can do likewise (Edin & Johansson, 1995; Collins & Prochazka, 1996; Collins *et al.* 2000).

Less attention has been given to potential interactions between the contributors to proprioception, yet such interactions are likely to occur under normal conditions. A long-standing proposal is that the input from cutaneous afferents has a minor role in signalling joint movement and that its major effect is by 'facilitation of the central action of intramuscular and joint receptors, rather than a specific individual role' (McCloskey, 1999). This view arose because 'disengagement' of muscles acting at the distal joint of one finger (by changing the position of the adjacent fingers) markedly impaired the detection of passively applied movements to the distal interphalangeal joints (Gandevia & McCloskey, 1976; Gandevia *et al.* 1983b), and this effect was even greater with anaesthesia of the joint (Ferrell *et al.* 1987; Clark *et al.* 1989). Anaesthesia of digital nerves (to eliminate the input from joint and distal cutaneous receptors but preserve that from intramuscular receptors in the forearm) also markedly impaired detection (e.g. Brown *et al.* 1954; Merton, 1970; Gandevia & McCloskey, 1976; Refshauge *et al.* 1998). Thus, performance deteriorated with removal of either the muscle or the cutaneous (plus joint) input. However, microneurographic recordings from cutaneous afferents innervating the glabrous skin of the hand suggested that these receptors provide ambiguous information about angular position (Hulliger *et al.* 1979; Burke *et al.* 1988). One way to rationalise these data with the prevailing views about the pre-eminence of muscle afferents was to ascribe the result with digital anaesthesia to loss of a general facilitation of detection. Preliminary evidence for this view arose because movement detection at the distal interphalangeal joint of the middle finger was worse in two out of three subjects when the adjacent fingers were anaesthetised (Gandevia & McCloskey, 1976). More recently, it has been shown that cutaneous receptors are used in the perception of movement at individual finger joints (Collins & Prochazka, 1996; Collins *et al.* 2000), although this does not preclude an additional facilitatory role. There is ample neural substrate for an interaction between various proprioceptive inputs, given that there is convergence at cortical and subcortical levels between cutaneous, joint and muscle afferents (e.g. Lemon & Porter, 1976; Millar, 1979; Maendly *et al.* 1981) and between inputs from adjacent fingers (e.g. Darian Smith *et al.* 1979; Gandevia *et al.* 1983a; Smits *et al.* 1991; Istvan & Zarzecki, 1994).

To date, there have been few further attempts to establish formally the existence of the proposed facilitation. The studies have been inconclusive and involved only small numbers of subjects. In support of the hypothesis, the detection of index finger movements was impaired by anaesthesia of the tip of the index finger in five subjects (the total tested), and by anaesthesia of the adjacent thumb in three subjects (also the total tested; Clark *et al.* 1986). However, this could not be confirmed when similar movements were studied during anaesthesia of both the

adjacent thumb and middle finger in two subjects (Ferrell & Smith, 1988), or the more remote ring and little fingers in two subjects (Clark *et al.* 1985).

Therefore, the experiments described herein were designed to seek evidence for the facilitation of proprioceptive performance at one digit by input from cutaneous receptors in adjacent digits. Subjects reported the direction of imposed movements in one study when cutaneous (and joint) input was removed from the adjacent digits, and in another study when cutaneous input was artificially increased. We hypothesised that proprioceptive performance would decrease when cutaneous input was removed, and improve when it increased. The index finger was selected as the digit to be moved because of its important interaction with the thumb in manual tasks and because input from the thumb can alter some aspects of its proprioceptive performance, such as force judgements (e.g. Gandevia & McCloskey, 1977), and the detection of cutaneous stimuli (Gandevia *et al.* 1983a).

METHODS

Two main studies were conducted and for each, supplementary experiments were added. The perception of movements imposed at the proximal interphalangeal joint of the index finger was investigated when cutaneous input was removed from the digits adjacent to the test digit using anaesthesia, and when input from the digits was artificially increased by electrical stimulation. A total of 30 healthy volunteers (12 female, 18 male) aged between 26 and 47 years participated, with some involved in more than one study. Each experiment lasted 1.5–3.0 h. All experiments conformed with the Declaration of Helsinki, written informed consent to participate was obtained from each of the volunteers and the studies were approved by the University of NSW human ethics committee.

Experimental arrangement

In the main studies, flexion and extension movements were imposed about the proximal interphalangeal joint of the left index finger (Fig. 1). The left forearm and hand were supported on a padded splint, with the wrist positioned in neutral supination-pronation and comfortable extension (~15 deg), and the metacarpophalangeal joint of the index finger was flexed to ~45 deg. The initial position of the proximal interphalangeal joint was the middle of its flexion/extension range (~45 deg). The middle phalanx was coupled to a linear servomotor by a 'clamp' over the sides, but not the dorsal or palmar surfaces of the digit. The proximal phalanx was stabilised by a clamp applied to its sides so that movement was confined to the proximal interphalangeal joint. Both actual angular displacement and geometric calculation were used to calibrate the equipment prior to data collection. Subjects were blindfolded or closed their eyes so that they could not see the hand or apparatus, and the use of earmuffs eliminated auditory cues. Subjects were not given feedback about their performance.

Standard protocol

Flexion and extension movements of ~5 deg were imposed about the proximal interphalangeal joint of the index finger from an initial position of ~45 deg flexion. Each movement was held at its full excursion for 3 s to allow time for a response. The joint was

then returned to the initial angle at a velocity of 3 deg s^{-1} . Ten flexion and 10 extension movements were imposed in random order. Subjects were instructed to nominate the direction of movement only when they were certain, and responses were only accepted before the finger had returned to the initial position. Subjects were regularly reminded to remain relaxed. We used this protocol because it is a conventional method for testing proprioceptive acuity (e.g. Gandevia & McCloskey, 1976; Hall & McCloskey, 1983) and it has a low rate of false positives. Subjects received the same instructions before all tests.

Removal of inputs from adjacent digits

In the first main study, feedback from the tips of the digits adjacent to the index finger was removed by digital nerve anaesthesia in 16 subjects. Only the tips were anaesthetised because it has been suggested that this skin may be the most important source of facilitatory inputs (Clark *et al.* 1986). Lignocaine (1–2 ml 1%, without adrenaline) was injected around each digital nerve, proximal to the distal interphalangeal joint in the middle finger, and in the midregion of the proximal phalanx in the thumb. A firm band was applied at the base of the digit to prolong the block. The block was considered complete when the sensation of light touch was lost, at which time other cutaneous modalities of sensation were also blocked.

Proprioceptive acuity was tested using a standard protocol under three conditions: first, the control condition with all inputs available; second, during anaesthesia of one adjacent digit (the thumb or middle finger, randomly assigned); third, during anaesthesia of both adjacent digits. Three velocities were tested for each condition: 1.25, 2.5 and 5 deg s^{-1} , in random order.

Since anaesthesia of the tips of the adjacent digits did not affect the ability to detect movement (see Results), in a supplementary experiment we blocked the median nerve at the wrist to remove the inputs from much of the palm and at least three fingers (three subjects). Movement detection was measured at the proximal interphalangeal joint of the sentient little finger, before and during the complete anaesthetic block at the wrist (9–12 ml, bupivacaine 0.5% and lignocaine 2% without adrenaline). The standard test protocol was applied to the little finger: movements of 5 deg magnitude were imposed on the proximal interphalangeal joint in blocks of a random mix of 10 flexion and 10 extension movements. The proximal phalanx was stabilised with a clamp and the middle phalanx was coupled to the motor to confine movement to the proximal interphalangeal joint.

Increase in input from adjacent digits

In the second study, we compared proprioceptive acuity at the index finger with and without artificially increased input from the adjacent digits ($n = 15$). The digital nerves were stimulated (50 Hz, 1 ms pulses) via surface electrodes ($\sim 40 \text{ mm} \times 10 \text{ mm}$, 3M, no. 1180) on the sides of the distal phalanx of the stimulated digits. Stimulation was delivered simultaneously to the thumb and middle finger for 6–8 s and began 1–3 s prior to movement onset. It was delivered in 50% of the movements in random order. Three stimulation intensities were used: perceptual threshold (PT), below PT ($\sim 0.9 \text{ PT}$) and above PT ($\sim 1.5 \text{ PT}$). At 1.5 PT, subjects perceived the sensation as 'strong but not uncomfortable, and radiating throughout the digit tip'. PT was defined as the intensity at which subjects could just detect a 2–3 s train of pulses. The different stimulus intensities were tested in random order.

Proprioception was tested at one velocity for each subject. The velocity selected was that at which subjects could identify correctly

approximately half of the imposed movements of 5 deg, and therefore varied among subjects (median, 1.0 deg s^{-1}). Movements were presented in blocks of 20, with stimulation delivered during 10 of the movements. One stimulus intensity was delivered during each block and each intensity was tested four times (i.e. four blocks of 20 movements for each stimulus intensity).

To investigate further the changes in detection with stimulation of the adjacent digits, a supplementary experiment was conducted in eight subjects. The stimulation was delivered at $\sim 1.5 \text{ PT}$ in randomised blocks of trials to one of three sites: the tip of the moving digit (i.e. index finger), the tip of the little finger on the ipsilateral hand, or the tip of the contralateral little finger.

As electrical stimulation impaired performance when delivered above PT (see Results), in a further supplementary experiment ($n = 10$ subjects) we increased the input with a natural stimulus. A small motor was used to rotate a brush that continuously stroked the tips of the adjacent digits. In one subject we established that the natural stimulus could not be detected when the digits to which the brushing was applied were anaesthetised with a clinically complete digital nerve block. A random mix of 10 flexion and 10 extension movements was imposed at the proximal interphalangeal joint of the test index finger with and without application of the brush stimulus. The velocity of the imposed movements was selected as that at which subjects could detect $\sim 60\%$ of control movements, usually 1.5 deg s^{-1} .

Data analysis

Detection of extension movements was slightly, but significantly worse than flexion movements in the two main studies (each: $P < 0.01$), therefore flexion and extension data were examined separately. Comparisons were made between conditions for each study using a two-way repeated-measures ANOVA. Further comparisons of significant results were made using the Bonferroni correction procedure. A one-way ANOVA was used to compare performance before and during median nerve block at each of the three velocities. Statistical significance was set at $P < 0.05$.

RESULTS

To investigate a possible facilitatory role in the detection of movement at one finger by afferents innervating remote digits, we measured proprioceptive acuity when cutaneous (and joint) input was removed and when it was increased from the digits adjacent to the 'moved' digit.

Removal of digital nerve inputs from adjacent digits by anaesthesia

Detection of passively applied flexion and extension movements at the proximal interphalangeal joint of the index finger improved with increasing velocity of movements under control conditions and during anaesthesia of one or both adjacent digits ($n = 16$; ANOVA, $P < 0.001$). Complete anaesthesia of the tip of one digit adjacent to the test index finger did not alter the detection of flexion or extension movements ($P = 0.15$ and $P = 0.43$, respectively), and neither did anaesthesia of the tips of both adjacent digits ($P = 0.167$ and $P = 0.306$, respectively) at any of the three test velocities. Group data are shown in Fig. 2.

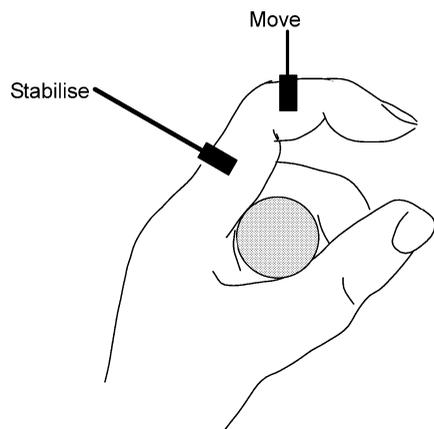


Figure 1. Experimental arrangement used to impose movements at the proximal interphalangeal joint (PIP) of the index finger

The proximal phalanx was stabilised with a clamp, and the middle phalanx was moved by a motor. The PIP joint was positioned at 45 deg flexion. The remaining digits, hand and wrist were stabilised in a standard position against a cylinder.

One reason for the lack of an effect of removal of digital nerve input may be that it did not remove the input from a sufficient number of tonically active receptors. To assess this, we measured proprioceptive performance at the proximal interphalangeal joint of the little finger at three velocities before and during anaesthetic block of the median nerve at the wrist. This procedure removed input from much of the hand, but it left the little finger intact. The muscles innervated by the median nerve were also paralysed. The median nerve block caused no change in acuity for detection of either flexion or extension movements (Fig. 3).

Increase in digital nerve inputs from adjacent digits

Simultaneous stimulation of the tips of the two digits adjacent to the test index finger, significantly reduced the detection of both flexion ($P = 0.002$) and extension movements ($P = 0.004$; Fig. 4) when delivered above PT (~ 1.5 PT, see Methods). The reduction was similar for flexion (55%) and extension (45%) movements. Stimulation had no effect on proprioceptive acuity when delivered below PT for flexion ($P = 0.215$) or extension movements ($P = 0.635$). However, stimulation at PT

slightly reduced the detection of flexion ($P < 0.001$), but not extension movements ($P = 0.328$).

To determine whether the reduced performance during suprathreshold stimulation of digits adjacent to the test digit was simply due to mental 'distraction' or to an interaction between the artificially increased input and the proprioceptive feedback from the moving digit, detection was measured under control conditions and when the left or right little finger or the test index finger was stimulated during movement. When the index finger was stimulated using an intensity above PT (~ 1.5 PT), proprioceptive performance decreased for both flexion ($P = 0.02$) and extension movements ($P = 0.02$). However, stimulation of either the ipsilateral or contralateral little finger did not affect proprioceptive performance (Fig. 5).

One explanation for decreased performance during electrical stimulation may be that the electrical stimulus did not provide a natural or coherent input. To assess this, we measured proprioceptive performance at the proximal interphalangeal joint of the index finger with and without a natural brushing stimulus applied to the tips of the adjacent digits. This natural stimulation of the adjacent

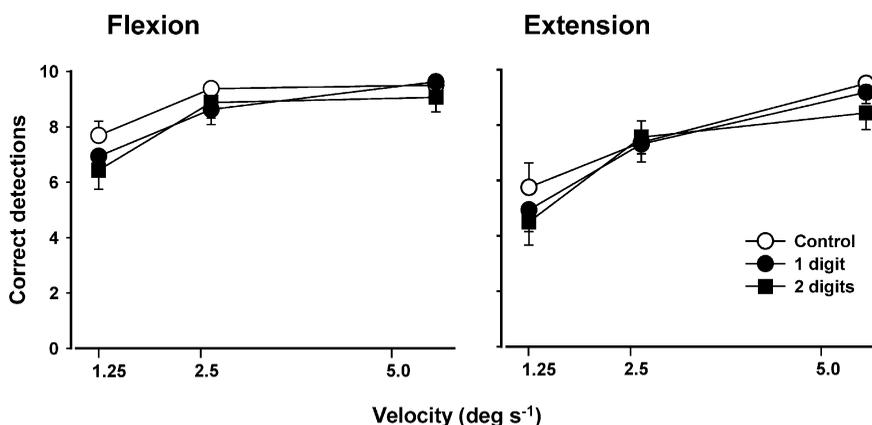


Figure 2. Detection of movements at the index finger before and during anaesthesia of adjacent digits (mean \pm S.E.M.)

There was no difference in the perception of movement imposed at the PIP joint of the index finger in the control condition with all inputs available (○), when the tip of one adjacent digit was anaesthetised (●) or when the tips of both adjacent digits were anaesthetised (■).

Figure 3. Detection of movements at the little finger during median nerve block (mean ± S.E.M.)

The detection of movements imposed at the little finger during median nerve block is shown for the three individual subjects tested. There was no clear effect of the anaesthesia on movement detection.

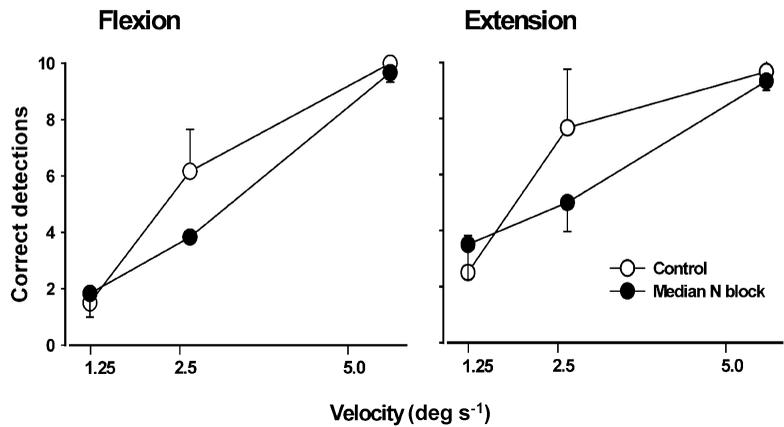


Figure 4. Detection of movements at the index finger during electrical stimulation (mean ± S.E.M.)

The test index finger was stimulated electrically (elec stim) at three intensities: below PT, at PT and above PT. For each stimulus intensity (■), a control condition (□) was tested. Stimulation of the test index finger affected the perception of flexion movements at PT, and both flexion and extension at intensities above PT. Electrical stimuli delivered at intensities below PT had no effect.

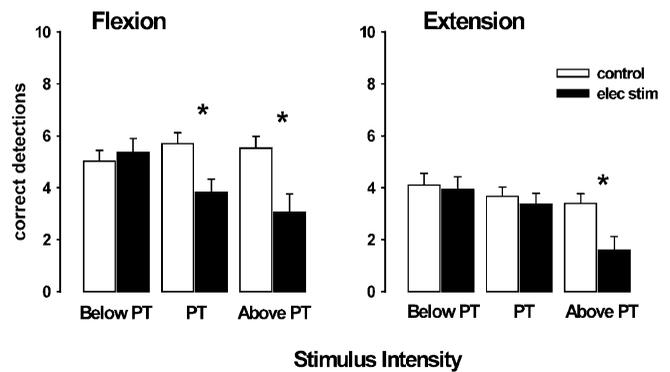


Figure 5. Detection of movements imposed at the index finger during a distraction electrical stimulation (mean ± S.E.M.)

Electrical stimulation was applied to the index finger, the ipsilateral little finger (Little) or the contralateral little finger. Stimulating the little finger on either hand did not alter detection of movement. Stimulation of the test index finger significantly reduced the ability to perceive both flexion and extension movements.

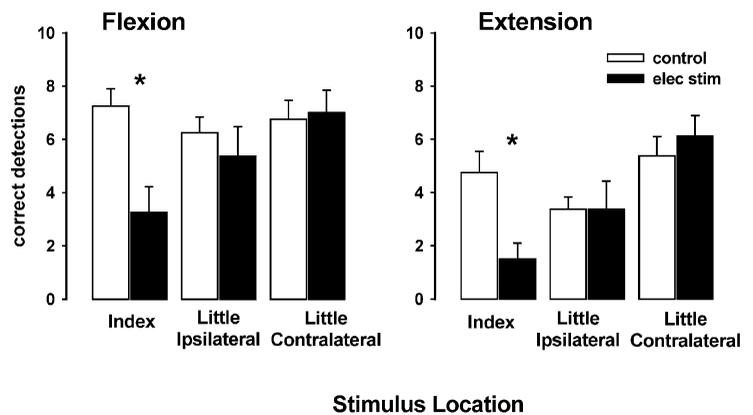
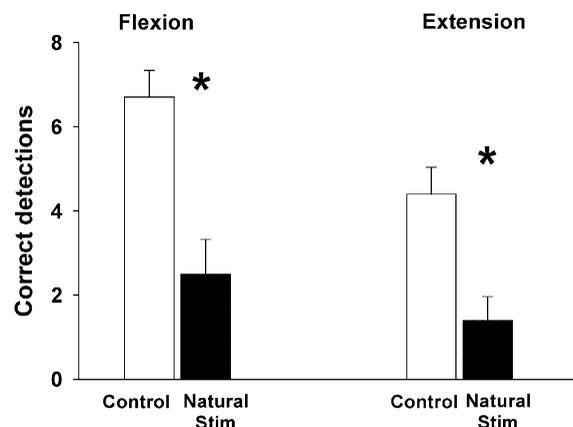


Figure 6. Detection of movements imposed at the index finger during natural stimulation (mean ± S.E.M.)

Natural stimulation (Natural stim) was applied by simultaneously brushing the tips of the middle finger and thumb. Natural stimulation of the digits adjacent to the test index finger (■) significantly reduced the ability to perceive both flexion and extension movements compared with control (□).



digits also significantly reduced the detection of both flexion and extension movements ($P = 0.018$; Fig. 6).

DISCUSSION

The detection of movements applied to the index finger did not diminish when the digital nerve input from adjacent fingers was removed, and detection did not improve when it was increased. Together, these findings suggest that a generalised facilitation by such inputs does not operate, at least at the proximal interphalangeal joint. The present findings represent the first detailed examination of the putative 'facilitation' of movement detection at the fingers.

Since movement detection was not impaired by loss of tonic inputs from the skin and joint afferents of adjacent digits, these inputs cannot be critical for normal detection at the index finger. Furthermore, anaesthesia of at least three digits (and some muscle afferents) with a median nerve block did not impair the detection of movements applied to the little finger. Thus, the tonic neural input from various digits does not, under resting circumstances, provide a detectable facilitation of the central circuits involved in detection of passive movements.

Electrical stimulation below PT of the adjacent digits did not alter detection. However, since the input from a single afferent is thought to be detectable, at least for afferents innervating the tips of the digits (e.g. Schady & Torebjörk, 1983; Vallbo *et al.* 1984; Macefield *et al.* 1990), it is possible that stimulation just below PT (i.e. stimuli that subjects were unable to perceive) may have increased input only minimally, if at all. Against this, the detection of a liminal stimulus to one digit is markedly improved with a simultaneous stimulus to the adjacent digit, a finding consistent with central convergence (Gandevia *et al.* 1983a). Nevertheless, increasing cutaneous input by applying a continuous electrical stimulation at or above PT, or a more natural stroking stimulus, to digits adjacent to the test finger did not enhance the detection of passive movement at the test proximal interphalangeal joint. In fact, the suprathreshold input from adjacent digits impaired it. This impairment was not due to attention being diverted by stimulation of the adjacent digits, because stimulation of inputs from either little finger had no effect on detection at the index finger. Furthermore, the size of the impairment was consistent for the two types of stimuli. Thus, the additional input from adjacent digits may effectively add 'noise' to the neural circuits involved in movement detection.

We also found that an abnormal input from the test digit itself impaired the detection of movement at its proximal interphalangeal joint. This impairment could be due to the addition of noise to the neural circuits, the same mechanism

suggested to explain the impaired performance during increased input from adjacent digits. Furthermore, the suprathreshold stimulation may have produced an ambiguous signal by activating some local cutaneous (and joint) afferents, which normally aid the detection of both flexion and extension movements at the proximal interphalangeal joint. Given that cutaneous afferents signalling skin stretch can contribute to movement detection (e.g. Edin & Johansson, 1995; Collins & Prochazka, 1996; Collins *et al.* 2000), such mechanisms are likely to contribute to the deficit.

There is agreement that joint, cutaneous and muscle afferents all contribute to movement detection, at least for the proximal interphalangeal joint of the digits, although the relative contribution of each class of afferent to movement detection remains a matter of debate (see Introduction). Taken together, our findings suggest that tonic cutaneous (and joint) input from digits adjacent to the moving digit is not essential for normal movement detection, while sustained enhancement of this input (but not more remote inputs) impairs detection. In light of these findings, the profound deficit in movement detection found by Gandevia & McCloskey (1976) and Refshauge and colleagues (1998) on the removal of cutaneous (and joint) input at the distal interphalangeal joint is likely to reflect the inadequate input by muscle afferents for normal movement perception.

As indicated in the introduction, the previous evidence for a general facilitation of movement detection is equivocal and comes from several studies, each involving only a few subjects. Those studies were primarily concerned with other aspects of the mechanisms involved in the detection of joint movement and position. However, while the present study has found no evidence for such a facilitation, it has revealed a novel effect in which input from adjacent, but not remote, digits impairs movement detection. Clearly, there is some interaction among the various proprioceptive inputs from the fingers, but not a general facilitation of the type originally proposed.

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