Closing in on the Neural Mechanisms of Finger Joint Angle Sense. Focus on “Quantitative Analysis of Dynamic Strain Sensitivity in Human Skin Mechanoreceptors”

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Investigation of the neural mechanisms of joint angle sense has a long, rich history in which the ideas have changed continually. The sense of joint angle was first thought to depend on joint receptors and then on muscle length receptors. More recently, skin receptors have been shown to be critical for sensing joint angle in the hand. The question that remains to be answered is which of the cutaneous receptors is responsible for sensing finger joint angle. In this issue, Ben Edin (p. 3233–3243) has taken the first step by calculating the skin strain and strain rates associated with joint movements and then applying those strains to cutaneous receptors to obtain an accurate statistical description of the neural activity that accompanies joint movement. The next step which remains to be done is to reconstruct the neural activity associated with specific psychophysical experiments to determine which receptor types can and which cannot account for the discrimination performance demonstrated in those experiments.

Since the time of Sherrington it has been known that joint movements activate joint, skin, and muscle receptors and that each might therefore play a role in the control and perception of joint angle. However, it has been difficult to narrow the possibilities, especially for joints in the hand, which is so dextrous. In the last decade or so, Ben Edin and others have focused on the role of skin receptors in the hand and have shown that they have a primary role in the perception of finger joint angle. In this issue, Ben Edin (2004) broaches, for the first time, the question of which of those cutaneous afferents can and which cannot account for human ability to discriminate finger position.

The pursuit of the neural mechanisms of joint angle perception has a long, rich history. In the 1960s, there was near universal agreement that joint receptors are responsible for joint angle perception (Goodwin et al. 1972b). What could be more obvious? The joints are richly innervated with sensory receptors, and they are ideally located to signal joint angle. Signals from the muscles and skin are indirect and fraught with complications. However, almost immediately the evidence weighed in heavily against joint receptors. In 1969, Burgess and Clark showed that the vast majority of joint receptors respond only at the extremes of extension and flexion and that they signal joint angle poorly at intermediate angles (Burgess and Clark 1969; Burke et al. 1988; Clark and Burgess 1975). In 1979, Clark et al. showed that anesthetizing the receptors of the knee joint capsule and the surrounding skin had no effect on the human ability to judge and discriminate joint angle. In the meantime, Goodwin et al. (1972a) had shown that vibratory stimuli (that activate muscle spindles strongly) applied to the tendons of biceps or triceps muscles alter the perceived elbow angle by as much as 40°. Thus within a decade the joint receptor lost its central role almost completely (Proske et al. 1988) and joint angle perception seemed to depend almost exclusively on muscle spindles (Matthews 1982). Note, however, that Ferrell has repeatedly presented evidence that the joint receptor plays a role, albeit a tertiary role (e.g., Ferrell et al. 1987).

Toward the end of the 1970s it became clear that joint angle perception in the hand is more complex. The phalangeal and metacarpal joints provide the hand with 20 degrees of freedom. It is, perhaps, unreasonable to expect that muscle spindles alone could bear the whole load in a structure as complex as the hand. In 1976, Gandevia and McCloskey showed that when the tendons of the middle finger are entrapped so the extensor and flexor muscles are functionally disconnected from the distal phalanx, subjects still have a substantial joint angle sense. The dynamic joint angle sense is reduced, but the static joint sense is, in fact, unaffected by the entrapment maneuver (Taylor and McCloskey 1990). (The entrapment is achieved by extending all the fingers and then flexing only the middle finger, which paralyzes the distal phalanx but leaves it free to be moved passively.) This suggested a role for skin receptors. Shortly thereafter, Hulliger et al. (1979) did show that all of the cutaneous mechanoreceptors of the palm are activated strongly by the skin stretch that accompanies finger joint movements. That set the stage for the last two decades in which the principal focus has been on the relative roles of the skin, joint, and muscle receptors in finger joint position sense.

In 1991, Ben Edin shifted the focus of attention to the skin of the back of the hand (Edin and Abbs 1991). A sound rationale for that shift is that the skin of the palm is frequently occupied by complex stimuli during tasks that require accurate perception of hand conformation, whereas the skin of the back of the hand is free to sense the skin stretch related to joint position. He showed that, as in the palm, all the cutaneous mechanoreceptor types are sensitive to the skin stretch produced by joint movement (Edin and Abbs 1991). Perhaps more interesting is his demonstration that cutaneous mechanoreceptors are at least as sensitive to joint angle changes as muscle spindles (Edin 1992; Edin and Vallbo 1990). This demonstrated the sufficiency but not the necessity of cutaneous receptors. Later, elegant psychophysical experiments by Edin and Johansson (1995), Collins and Prochazka (1996), and Collins et al. (2000) showed that skin stretch near the finger joints produces the illusion of movement and that it interacts with sensory information provided by the muscles to direct the sense of movement to the appropriate finger. Thus a role for
skin receptors in the perception of finger joint position is well established.

The outstanding question is which cutaneous receptors provide the relevant information. In this issue, Edin (2004) reports a very careful study of the static and dynamic sensitivity of each the principal receptor types to skin stretch. Among the different receptor types reported by Edin, the SAII afferents would appear to have the quantitative properties most suited to the task but SAIII afferents [a new receptor class previously described by Edin (2001)] are a close second, and SAI and the rapidly adapting receptor types cannot be ruled out. The problem here, as in all studies of the neural mechanisms of tactile perception, is that all of the mechanoreceptors are very sensitive and all or most are activated by most stimuli. Sorting out the roles of each type in tactile perception has required a long period of combined psychophysical and neurophysiological investigation (reviewed in Johnson 2001, 2002).

There have been many psychophysical studies and many neurophysiological studies of joint angle sensitivity, but none of the neurophysiological experiments have been designed for the kind of hypothesis testing that is required to distinguish the roles of the different mechanoreceptors. Edin has taken the first step by calculating the skin strain and strain rates associated with joint movements and then applying those strains to cutaneous receptors to obtain an accurate statistical description of the neural activity that accompanies joint movement. The next step, which remains to be done, is to reconstruct the neural activity associated with specific psychophysical experiments to determine which receptor types can and which cannot account for the discrimination performance demonstrated in those experiments.

REFERENCES


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