Notes and Comment

A correction and a comment on Craig and Lyle (2001)

JAMES C. CRAIG
Indiana University, Bloomington, Indiana
and

KEITH B. LYLE
Yale University, New Haven, Connecticut

In a recent paper, Craig and Lyle (2001) measured tactile spatial acuity on the palm and compared these results with the results from similar measures on the fingertip. The changes in sensitivity between the two sites appeared to be consistent with estimates of the relative density of innervation between the two sites. Rather than compare their results with changes in the density of innervation, Craig and Lyle should have compared them with changes in the spacing between receptors. On this basis, psychophysical performance is much poorer on the palm than one would predict on the basis of the spacing between receptors. Some possible reasons are offered for the difference between the psychophysical results and the predictions based on receptor spacing.

In a recent paper in *Perception & Psychophysics* (Craig & Lyle, 2001), spatial acuity on the palm was determined with two different psychophysical measures, letter recognition and grating orientation. On the basis of these measures, it was estimated that letters on the palm had to be seven to nine times larger than letters on the distal phalanx (fingertip) to produce comparable levels of performance. The grating orientation thresholds were six to seven times larger on the palm than on the fingertip. In another study, grating orientation thresholds at the base of the finger (proximal phalanx) were about four times those measured at the fingertip (Craig, 1999).

What accounts for the reduced spatial acuity on the palm and the base of the finger? It has been suggested that density of innervation is a major limiting factor for spatial acuity (Johnson, Hsiao, & Twombly, 1995). Two studies, one with humans (Johansson & Vallbo, 1979) and one with monkeys (Darian-Smith & Kenins, 1980), have provided estimates of the density of innervation for several locations on the hand. Of the four types of afferents that respond to low-level mechanical stimuli in glabrous skin, slowly adapting, type I (SAI) afferents are thought to be responsible for conveying fine spatial information (John-

son & Hsiao, 1992). Estimates of the density of innervation of SAI afferents in humans are 70 per square centimeter on the fingertip, 30 per square centimeter on the rest of the finger, and 8 per square centimeter on the palm (Johansson & Vallbo, 1979). In estimating how much spatial acuity should decline when testing the palm, as compared with testing the fingertip, Craig and Lyle (2001) used the ratio of the densities of innervation. Between the fingertip and the palm this was 70 to 8, or 8.8 to 1. As has been noted, letters had to be seven to nine times larger and groove widths six to seven times larger on the palm, as compared with the fingertip. Craig and Lyle concluded that these changes in sensitivity between the two sites were within the range predicted by the estimated changes in density of innervation.

For registering spatial detail, the spacing between receptors is the critical measure (Johnson & Phillips, 1981). Rather than density of innervation, Craig and Lyle (2001) should have based their estimates on changes in spacing.¹ Spacing between receptors changes by the square root of the ratio of the densities. If the density of innervation decreases by a factor of 2, the spacing between receptors increases by the square root of 2, 1.414. To double the distance between receptors, the density of innervation must decrease by a factor of 4. Table 1 shows the estimated density of innervation for three locations on the hand, the corresponding spacing between receptors, and the thresholds for the grating orientation task. The spacing between receptors on the palm (3.5 mm) is about three times the spacing on the fingertip (1.2 mm), yet the grating orientation threshold increases by more than seven times (8.5 mm, the average threshold on the palm, divided by 1.2 mm, the threshold on the fingertip). Similarly, the spacing between receptors at the base of the finger is only one and one half times that at the fingertip, whereas the threshold increases by a factor of 4 (Craig, 1999). Thus, performance on spatial tasks is considerably poorer on the palm and the base of the finger than would be predicted by the estimated changes in peripheral innervation.

What might account for the psychophysical measures of spatial acuity's disagreeing quantitatively with the density of innervation (spacing) estimates? There are several possibilities. First, spatial acuity as measured by letter recognition and grating orientation is limited by more than the density of innervation. Second, the estimates of density of innervation are inaccurate.

The evidence that there is a close correspondence between psychophysical measures, such as letter recognition and grating orientation, and density of innervation is based, for the most part, on measurements done at the fingertip. In a series of studies, Johnson and his colleagues (Johnson & Phillips, 1981; Phillips, Johansson, & John-

This research was supported by National Institutes of Health Grant DC00095, National Institute on Deafness and Other Communication Disorders. Correspondence concerning this article should be sent to J. C. Craig, Indiana University, Department of Psychology, 1101 E. 10th St., Bloomington, IN 47405-7007 (e-mail: craigj@indiana.edu).

Table 1
A Comparison of Density of Innervation, Spacing Between Receptors, and Spatial Sensitivity at Three Locations

Site	Density (per cm ²)	Spacing (in mm)	Grating Orientation (mm)
Fingertip	70	1.2	1.2
Base of finger	30	1.8	4.8
Palm	8	3.5	8.5

son, 1992; Phillips & Johnson, 1981) have shown that of the four types of mechanoreceptive afferents in glabrous skin, only SAIs are capable of conveying the finest spatial information. Three psychophysical measures conducted on the distal fingertip—letter recognition, grating orientation, and gap detection—showed similar psychometric functions. Moreover, the relative sensitivities for the three measures fell roughly in the ratio of 5 to 2 to 1 (letter height to grating period to gap) and were consistent with the estimates of the spacing between receptors for the fingertip (Johnson & Philips, 1981). Additional neurophysiological recordings from first-order afferents in monkeys (Phillips & Johnson, 1981) and in humans (Phillips et al., 1992) provided evidence that SAI fibers, and only SAI fibers, convey a faithful spatial image of the stimulus object presented to the skin. Below the limits of psychophysically determined spatial sensitivity, the peripheral spatial image appears to fail to convey the information needed to identify the pattern. The strong inference was that spatial sensitivity is limited by the quality of the peripheral image and that, in turn, is limited by the spacing between receptors.

This limitation may be special for the fingertips. As a number of investigators have pointed out, the fingertips are heavily involved in haptic exploration (Johansson & Vallbo, 1979; Johnson & Hsiao, 1992). To the extent that the use of a particular site is associated with central mechanisms capable of processing information, the fingertips should have one of the most highly developed central mechanisms. If central mechanisms do limit processing, it would most likely be a limitation at sites other than the fingertips.

If central mechanisms are limiting performance at the palm, training might be expected to improve performance, and it does, particularly on a letter identification task. Over a period of 25 to 30 sessions, letter identification improved from about 20% correct to about 60% correct (Craig & Lyle, 2001), and this occurred without feedback. However, practice also improves letter identification performance on the fingertip, increasing from 38% to 64% correct over 8 sessions. (Vega-Bermudez, Johnson, & Hsiao, 1991).

Craig and Lyle (2001) compared the types of confusions that occur with letter identification on the fingertip and on the palm. The similarity in the types of confusions led them to conclude that the letters were processed in the same way at the two sites. If central mechanisms are partly responsible for limiting performance at the

palm, the limitation appears to be quantitative, rather than qualitative, in nature.

Wheat and Goodwin (2000) have developed a model for spatial discrimination of tactile gratings that allows them to vary certain parameters and see the effect on discriminability. They note, somewhat surprisingly, that decreasing the density of innervation did not always result in their model's predicting a decline in discriminability and that other factors, such as the position of receptive fields, may affect performance. They comment specifically on the fact that spatial acuity declines with age (Stevens & Patterson, 1995) and speculate that aging might not produce a uniform loss in receptor density but, rather, might lead to a patchy distribution of receptors. Such a patchy distribution might produce a more severe perturbation in performance than that predicted by the overall change in density of innervation. It may be that, in moving from the fingertip to the palm, a similar patchy distribution occurs and a more severe decline in spatial acuity is the result.

With regard to the estimates of density of innervation, Johansson and Vallbo (1979) estimated that there are 11,564 large myelinated fibers in the median nerve that innervates the glabrous skin of the hand. In computing their estimates of the density of innervation, they sampled 334 fibers. Of these 334, 84 were identified as SAI fibers. From their results, it appears that of the 84, 55 had receptive fields in the distal fingertip, 23 in the rest of the finger, and 6 in the palm. Small sampling errors could lead to substantial changes in the estimated ratio of densities between the fingertip and the palm and might help explain the discrepancy between the psychophysical data and the estimated densities of innervation.

The psychophysical data do agree with the estimated density data in the following way: There is a decline in spatial acuity as the site of stimulation moves from the distal fingertip to other areas on the finger and to the palm (Craig, 1999; Craig & Lyle, 2001; Stevens & Choo, 1996). The decline in sensitivity, as measured by several techniques, is greater than that predicted by the decline in density of innervation and the resulting increase in spacing between receptors.

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NOTE

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