

# Tactile learning is task specific but transfers between fingers

K. SATHIAN and A. ZANGALADZE  
*Emory University School of Medicine, Atlanta, Georgia*

Practice-related improvement in visual perception is highly specific for properties of the stimulus used in training. We explored the specificity of such perceptual learning in the human tactile system, using gratings consisting of alternating ridges and grooves. Practice effects on grating discrimination showed limited transfer between grating sets defined by spatial variation in either groove width or ridge width, consistent with partially overlapping neural representations of these two spatial parameters. In contrast, substantial interdigital transfer of practice effects occurred for discrimination of gratings varying in either spatial parameter and also for spatial acuity-dependent discrimination of grating orientation. We conclude that tactile learning, although quite as task specific as in other sensory systems, generalizes with considerable facility across fingers, unlike visual learning, which is highly location specific.

Perceptual learning has been studied empirically for over a hundred years (Gibson, 1953). It is commonly studied in the laboratory in terms of improvement in perceptual performance with practice. The question of the degree of specificity of practice effects for the task used in training and the extent of transfer to other experimental conditions was pursued by early workers, with variable results (Gibson, 1953). More recent research on the visual system has established that perceptual learning, in a wide variety of tasks, is highly specific for the retinal location and numerous other properties of a visual stimulus (reviewed by Gilbert, 1994; Sagi & Tanne, 1994). For instance, the faster perception of depth in random-dot stereograms that occurs with repeated observations is specific to the retinal location of the stimulus (Ramachandran, 1976) and the orientation of its constituent elements (Ramachandran & Braddick, 1973). Similarly, practice-related improvement in performance is specific for grating orientation and spatial frequency in a task requiring discrimination of grating spatial phase (Fiorentini & Berardi, 1980) and for the retinal location and orientation of background elements in a task relying on preattentive texture discrimination (Karni & Sagi, 1991).

These findings have led to the suggestion that practice effects are mediated by plasticity in particular neuronal pools in primary visual cortex (Karni & Sagi, 1991; Gilbert, 1994). It has also been argued that specificity might involve top-down attentional selection (O'Toole & Kersten, 1992), reinvigorating an important aspect of Gibson's (1969) description of the process of perceptual learning. Although other sensory systems have not been studied as intensively, the specificity of perceptual learning is apparently not confined to the visual system. For instance, improvement in auditory frequency discrimination in nonhuman primates was found to be specific to tone frequency (Recanzone, Schreiner, & Merzenich, 1993).

Much attention has been devoted to the neural correlates of perceptual learning and other forms of neural plasticity. Reorganization of topographic maps in the relevant primary sensory cortex was reported to accompany learning in the auditory (Recanzone et al., 1993) and somatosensory systems (Recanzone, Merzenich, & Jenkins, 1992; Recanzone, Merzenich, Jenkins, Grajski, & Dinse, 1992). Improvement in tactile discrimination of vibratory frequency (Recanzone, Jenkins, Hradek, & Merzenich, 1992) was correlated with sharpening and intensification of neuronal activity in primary somatosensory cortex (Recanzone, Merzenich, & Schreiner, 1992). Recent reviews have summarized evidence for similar map reorganization in response to various forms of deafferentation (Kaas, 1991), for dynamic modifiability of somatosensory maps (Weinberger, 1995), and for the proposal that changes in synaptic efficacy according to the Hebbian rule underlie these diverse neural phenomena (Merzenich & Sameshima, 1993).

Despite this tremendous interest in neural plasticity, particularly in the somatosensory system, there is no clear picture of the specificity of tactile learning. Learning effects in vibrotactile pattern identification on the fingerpad reportedly transfer outside the conditions of initial

---

Our findings were reported at the 25th annual meeting of the Society for Neuroscience in San Diego (Sathian & Zangaladze, 1995). This work was supported in part by a grant from the NINDS (1R29NS34111) to K.S. A.Z. is supported by the Campbell Foundation. Yashpal Matharu wrote software used to generate artwork for gratings. Photographic support was provided by Emory University's Medical Illustration Unit. Gratings were photo-etched at Flexocraft, Inc., College Park, GA. Dale Rice and Omar Wadi of the Medical Engineering Unit at Emory Hospital provided machining support to cut the gratings and make the holding plates. We thank Gargi Patel for helping to run some of the experiments. Most of all, we thank our subjects for their participation. Correspondence should be addressed to K. Sathian, Emory University School of Medicine, Department of Neurology, WMRB-6000, P.O. Drawer V, Atlanta, GA 30322 (e-mail: sathian@neuro.emory.edu).

training (Craig, 1988; Epstein, Hughes, Schneider, & Bach-y-Rita, 1989). Early studies on two-point discrimination on the forearm suggested that practice effects transfer outside the trained zone to homologous areas contralaterally (Dresslar, 1895; Mukherjee, 1933) but not to surrounding areas (Dresslar, 1895). Others (Recanzone, Jenkins, et al., 1992) have emphasized that practice-related improvement in vibratory frequency discrimination is specific, albeit incompletely, for the trained finger. It was therefore of interest to pursue, psychophysically, the specificity of tactile learning, as a prelude to neurobiological study.

Texture perception emerges from introspective (Darian-Smith, 1984) and empirical observations (Heller, 1989; Klatzky, Lederman, & Reed, 1987) as a prime aspect of the tactile sense. Gratings, consisting of alternating ridges and grooves, were first introduced into the psychophysical study of tactile texture perception by Lederman and Taylor (1972) and subsequently have been employed in numerous psychophysical and neurophysiological studies of the tactile system (reviewed by Sathian, 1989). We therefore used such gratings to study the task and location specificity of perceptual learning in the tactile system.

## EXPERIMENTS 1 AND 2

### Learning to Discriminate Gratings

The tactile texture (roughness) of gratings can be manipulated by varying either their groove width (GW) or their ridge width (RW) (Lederman & Taylor, 1972; Sathian, Goodwin, John, & Darian-Smith, 1989). Grating roughness increases as GW increases or, less markedly, as RW decreases, suggesting that the relevant neural processes might differ for these two spatial parameters. Neurophysiological studies indicate that, in fact, partially overlapping peripheral neural mechanisms are involved. Changes in GW but not RW are reflected in the mean firing rate of tactile primary afferents (Sathian et al., 1989). The afferents fire in bursts whose frequency equals grating temporal frequency. The number of impulses per burst is affected by variations in either parameter: the effects of GW but not RW are independent of concomitant changes in grating temporal frequency (Goodwin, John, Sathian, & Darian-Smith, 1989). Moreover, for 2-D dot patterns, changes in element size—analogueous to grating RW—evoke smaller variations in a number of neural response measures, including the spatial profile of discharge in the afferent pool, than do changes in interelement spacing—analogueous to grating GW (Connor, Hsiao, Phillips, & Johnson, 1990). Overall, it appears likely that afferent response intensity (probably reflecting the extent of skin deformation), as well as its spatiotemporal patterns (reflecting corresponding stimulus patterns), contributes to the perception of changes in GW, whereas perception of changes in RW depends on spatiotemporal response patterns.

We used two grating sets, one distinguished by variations in GW and the other by variations in RW, to examine task and location specificity in learning to discriminate between gratings.

## General Method

### Subjects

Neurologically normal volunteers with callus-free hands were recruited after their informed consent was obtained. Subjects were paid for their participation at an hourly rate.

### Gratings

Steel-backed plastic gratings were manufactured along the lines of methods detailed elsewhere (Darian-Smith & Oke, 1980). Briefly, artwork was generated at  $4.25\times$  magnification on a high-resolution laser printer ( $1,200 \times 1,200$  dpi) using custom software running on a PC. A matte negative of the patterns, photographically reduced to actual size, was employed as a mask in a commercial process using ultraviolet light to photo-etch a photosensitive, steel-backed, plastic plate (Toyoba Printight), out of which the resulting gratings, measuring  $80 \times 40$  mm, were subsequently cut. Gratings were examined under a microscope, and those with burrs or other imperfections attributable to the etching process were rejected.

Grating spatial parameters were measured to an accuracy of 0.01 mm: the nominal and actual values are given in Table 1. One set of gratings varied in GW, with RW constant. The other set varied in RW while GW was constant. In each set, the grating with the greatest value of the varying spatial parameter (nominally 2.0 mm) was designated as the standard. On the other, comparison, gratings, the variable parameter was less than that on the standard by an amount ( $\Delta$ ) that was used as the independent variable in psychometric functions. The ranges of grating spatial parameters correspond to those used in earlier studies (Sathian, 1989).

**Table 1**  
Values (in Millimeters) of Grating Spatial Parameters  
in Experiments 1 and 2

	GW		RW		$\Delta$ Actual
	Nominal	Actual	Nominal	Actual	
GW-Varying Set					
Standards	<i>2.0</i>	<i>1.97</i>	0.2	0.20	0
	<i>2.0</i>	<i>1.97</i>	0.2	0.18	0
Comparisons	<i>1.95</i>	<i>1.93</i>	0.2	0.18	0.04
	<i>1.9</i>	<i>1.89</i>	0.2	0.19	0.08
	<i>1.8</i>	<i>1.82</i>	0.2	0.18	0.15
	<i>1.7</i>	<i>1.74</i>	0.2	0.18	0.23
	<i>1.6</i>	<i>1.62</i>	0.2	0.17	0.35
	<i>1.5</i>	<i>1.50</i>	0.2	0.18	0.47
	<i>1.4</i>	<i>1.40</i>	0.2	0.18	0.57
	<i>1.2</i>	<i>1.22</i>	0.2	0.18	0.75
	<i>1.0</i>	<i>1.00</i>	0.2	0.20	0.97
	<i>0.75</i>	<i>0.75</i>	0.2	0.19	1.22
	<i>0.5</i>	<i>0.52</i>	0.2	0.18	1.45
RW-Varying Set					
Standard	1.0	1.00	<i>2.0</i>	<i>1.95</i>	0
Copies	1.0	1.04	<i>2.0</i>	<i>1.96</i>	0
	1.0	1.02	<i>2.0</i>	<i>1.94</i>	0
	1.0	0.97	<i>2.0</i>	<i>1.94</i>	0
Comparisons	1.0	1.00	<i>1.9</i>	<i>1.9</i>	0.05
	1.0	1.00	<i>1.8</i>	<i>1.79</i>	0.15
	1.0	1.01	<i>1.7</i>	<i>1.69</i>	0.25
	1.0	1.03	<i>1.6</i>	<i>1.60</i>	0.35
	1.0	0.97	<i>1.45</i>	<i>1.45</i>	0.5
	1.0	1.01	<i>1.3</i>	<i>1.30</i>	0.65
	1.0	1.02	<i>1.2</i>	<i>1.18</i>	0.75
	1.0	1.02	<i>1.0</i>	<i>1.02</i>	0.95
	1.0	0.99	<i>0.8</i>	<i>0.79</i>	1.15
	1.0	1.00	<i>0.5</i>	<i>0.50</i>	1.45

Note—Values for the parameter varying within a set are italicized. GW, groove width; RW, ridge width;  $\Delta$ , difference in varying spatial parameter between comparison and standard gratings.

Above the upper limits the grating can no longer be considered a continuous texture. The minimal values of  $\Delta$  are imposed by physical limitations of the manufacturing process.

Gratings were mounted on holding plates with stops at either end. Cylindrical magnetic plugs (Bunting Magnetics Co., Elk Grove Village, IL) were embedded in the plates, flush with their surfaces (Goodwin, Morley, Clarke, Lumaksana, & Darian-Smith, 1985). This enabled rapid changing of gratings but ensured their immobility while they were being scanned with the finger.

### Procedure

In each trial, subjects scanned a pair of gratings, using one fingerpad. No constraints were imposed on number, duration, or sequence of scans. Subjects were free to choose whatever movement speeds and contact forces they deemed appropriate (Morley, Goodwin, & Darian-Smith, 1983). However, use of the nail was not permitted, in order to restrict the population of stimulated receptors to cutaneous mechanoreceptors. Vision of the gratings and the scanning finger was excluded using suitable screens and low ambient light.

On the subject's left was the standard grating. The other grating was either a copy of the standard or a comparison grating that was constant within a block of 24 trials and varied between blocks. Subjects were asked to state whether the pair felt the "same" or "different." The two alternatives were equally probable, and trial sequences were randomized. Note that this discrimination of grating pairs does not call for an explicit judgment of texture; that is, it could well be achieved by simply comparing appropriate neural representations to determine whether they differ or not.

Two virtually identical standards were available for the GW-varying set (Table 1). Each of these was used as the left grating in alternating blocks while the other served as the remaining member of the *same* pair. For the RW-varying set, a standard and three closely similar copies were available (Table 1). In this case, the standard was always on the left and the three copies were used, with equal probability, as remaining members of the *same* pair. This design ensured that idiosyncratic imperfections of individual gratings would not serve as extraneous cues to aid discrimination.

Feedback on responses was not provided, because a considerable body of work shows that perceptual learning obtains in the absence of feedback (Gibson, 1953; McKee & Westheimer, 1978; Shiu & Pashler, 1992).

The form of two-alternative forced choice used was liable to be affected (and was in fact affected variably) by response bias. Therefore,  $d'$ , the bias-free separation index, was computed for each block, by transforming the false alarm and hit rates for *different* responses to  $z$  scores and subtracting the former  $z$  score from the latter (Lamb, 1983). The difference limen (DL) was taken as the  $\Delta$  value corresponding to a  $d'$  of 1.34, which corresponds to 75% correct, unbiased performance. Except where  $d'$  for a particular comparison grating was exactly 1.34, the DL for each session was determined from the psychometric function ( $d'$  vs.  $\Delta$ ) by linear interpolation between the two closest  $d'$  values on either side of this discrimination threshold (van Boven & Johnson, 1994a). Standard deviations ( $SDs$ ) were estimated for all  $d'$  values from binomial statistics (van Boven & Johnson, 1994a). Typically, these  $SDs$  did not overlap for the  $d'$  values from which the DL was calculated. When they did, proximate  $d'$  values provided adequate reassurance of the reliability of the threshold computation. Occasionally,  $d'$  was greater than 1.34 for the physically minimal  $\Delta$ , in which case the DL was taken as the minimum for the purposes of statistical analyses. Sessions generally lasted about an hour and consisted of four to six blocks.

As is usual in experiments of this type (Gibson, 1953), comparison gratings were presented in a sequence of overall increasing difficulty. The first comparison grating for a session was chosen on the basis of a few practice trials in the first session for each

subject; in subsequent sessions, this choice was guided by performance in the previous session. The goal within each session was to present a series of blocks with progressively smaller  $\Delta$  values until performance fell to or approached chance levels.

Perceptual learning was manifest as a progressive decline in DL over successive sessions, which were as far as possible on successive days (not including weekends). The final DL, the lowest achieved for a particular training sequence, was considered attained when the DL was stable (or increased) over two or more sessions or when the physical minimum was reached. The percentage decline in DL from its initial value was used as an index of the magnitude of practice effects. This effectively normalizes for any variations in initial DL. The number of sessions required to achieve the final DL was used to index the rate of learning. The extent of transfer of practice-related improvement from the first training sequence to a subsequent one was assessed by comparing these measures and the initial DLs between sequences. Repeated measures analysis of variance (ANOVA), performed using SAS, was utilized to assess statistical significance ( $\alpha = .05$ ) of the results.

## Experiment 1

The question addressed in Experiment 1 was as follows: Are practice effects specific for particular grating spatial parameters?

### Method

In this experiment, 5 subjects were first presented with the GW-varying set in successive sessions, followed by the RW-varying set, until optimal discrimination capability was achieved for each set in turn (see above). The order of sets was reversed for 4 other subjects. Data were also used from 2 additional subjects, one for the GW-varying set presented second and another for the RW-varying set presented first. The latter subject did not run with the GW-varying set, while data from the former subject on the RW-varying set could not be used owing to a prior unsuccessful attempt to induce perceptual learning of grating discrimination based on RW with another paradigm (see below). Hence, data were available for a total of 11 subjects, with 5 subjects running in each of the following four conditions: GW-varying set first; GW-varying set second; RW-varying set first; RW-varying set second. The design was thus balanced with respect to these four conditions. Two of the 11 subjects were left-handed; the rest were right-handed. Three subjects used their nondominant hand, and the rest, their dominant hand, to scan the gratings. The index fingerpad was always used in this experiment.

### Results and Discussion

Improvement in discriminative ability from the initial level was a general observation, regardless of grating set or presentation order. Almost all subjects demonstrated practice effects. As Figure 1 illustrates for typical individual subjects, practice with the first set clearly did not abolish learning effects for the second set.

Across subjects (Table 2), the percentage decline in DL was not significantly affected by presentation order ( $p = .72$ ), grating set ( $p = .56$ ), or the interaction between these two variables ( $p = .41$ ). The number of sessions required to achieve the final DL was also unaffected by presentation order ( $p = .21$ ), grating set ( $p = .21$ ), or their interaction ( $p = 1.0$ ). The lack of significant effect of presentation order on these dependent variables suggests considerable specificity of practice effects for

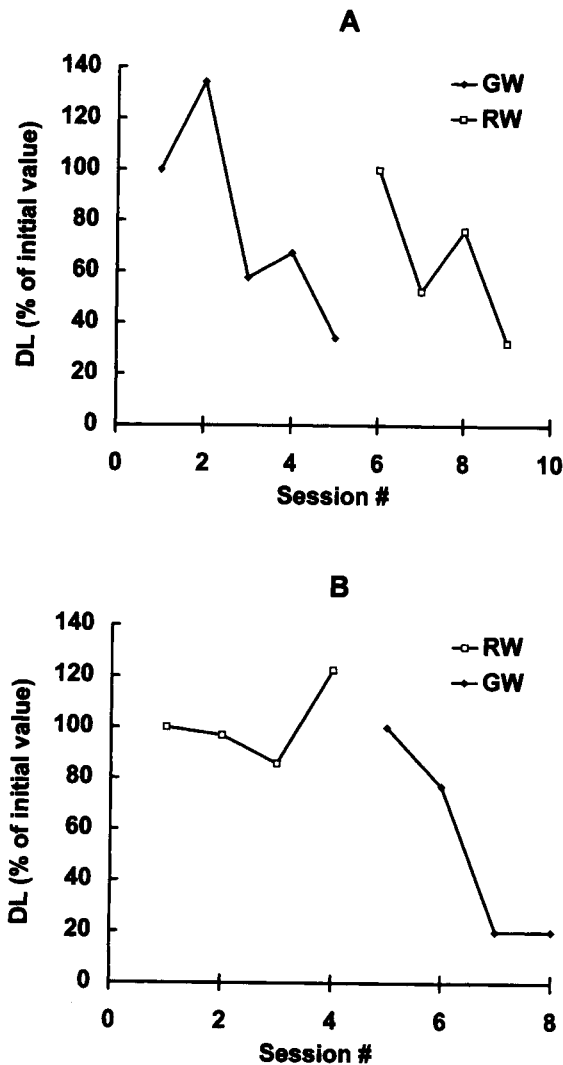


Figure 1. Difference limens (DLs) obtained for two representative individual subjects in successive sessions in Experiment 1, expressed as percentages of the initial DL for each set. (A) GW-varying set first, RW-varying set second. (B) RW-varying set first, GW-varying set second. GW, groove width; RW, ridge width.

the set used for training. Importantly, the lack of significant effect of grating set on these measures justifies pooling the results of this experiment across grating sets, rather than analyzing the effect of presentation order separately for each set, which would have required a larger *n*.

Initial DLs were significantly lower for each set when presented second rather than first (Figure 2, *p* = .04). This indicates that, despite the specificity noted in the preceding paragraph, limited transfer of practice effects did occur between grating sets. Initial DLs were also significantly lower for the GW-varying set than for the RW-varying set (Figure 2, *p* = .007). The interaction of grating set and order of presentation did not significantly affect this dependent variable (*p* = .53).

Taken together, the results of this experiment permit the conclusion that practice effects are incompletely spe-

cific to the spatial parameters (GW and RW) defining grating set. This is consistent with the neurophysiological evidence cited earlier that the peripheral neural representations of variations in these two spatial parameters differ in many respects but share some commonality (Connor et al., 1990; Goodwin et al., 1989; Sathian et al., 1989). In other words, the partially overlapping neural mechanisms permit partial transfer of learning effects between sets defined by the two spatial parameters. Owing to the relatively small number of subjects in each condition, a more quantitative assessment of the extent of transfer is not possible. Since the general tone of the conclusions of this experiment is consonant with the extensive literature on the task specificity of perceptual learning (Sagi & Tanne, 1994), this issue was not pursued further. It is worth noting, however, that we obtained similar results in preliminary experiments with a somewhat different paradigm, where gratings with cyclic spatial variations along their length were to be distinguished from a standard, uniform grating. Some subjects (including the 1 whose data were used only in the GW-second series) were unable to learn effectively with this paradigm, which was therefore abandoned in favor of that outlined above.

Discussion of the differences in DL between the GW- and RW-varying sets is postponed to the General Discussion of Experiments 1 and 2.

### Experiment 2

The question addressed in Experiment 2 was as follows: Are practice effects specific to the trained finger?

### Method

Initial training in this experiment proceeded as in Experiment 1. Following initial training on one index finger, subjects were tested on one or more other fingers: the contralateral index finger in all cases and one of the middle fingers in some cases. Five subjects ran with each grating set; 2 of them ran with both sets. Hence, a total

Table 2  
Magnitude and Rate of Learning

Experiment	<i>n</i>	Order	% Decline in Threshold		Number of Sessions	
			<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
1	5	GW: first	52.8	16.1	3.8	0.8
	5	GW: second	34.4	15.4	2.4	0.6
	5	RW: first	48.9	17.9	5.2	1.8
	5	RW: second	56.2	10.3	3.8	0.8
2	5	GW: first	65.6	10.6	4.0	0.3
	8	GW: subsequent	36.1	10.7	2.1	0.4
	5	RW: first	77.5	3.2	6.0	1.4
	8	RW: subsequent	46.6	12.7	2.5	0.6
3	8	First	32.0	7.3	3.1	0.4
	15	Subsequent	25.1	6.1	1.9	0.2
R	1	First	70		40	
	1	Subsequent	50		15	

Note—Discrimination thresholds for Experiments 1–3 are defined in the text. Experiment R refers to values extracted from Figure 7 in Recanzone, Jenkins, et al. (1992), for an owl monkey trained to discriminate vibratory frequency on its third and later its fourth digit; threshold expressed as difference limen (Hz). GW, groove width; RW, ridge width.

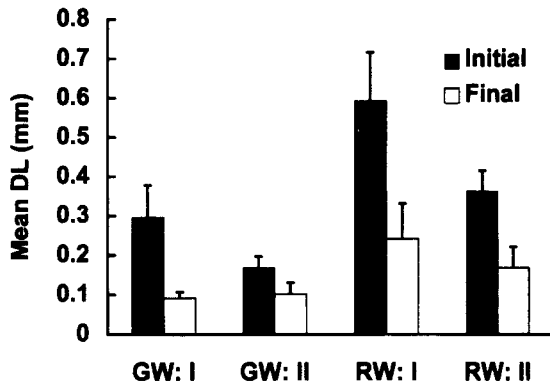


Figure 2. Mean initial and final difference limens (DLs) across subjects in Experiment 1. Bars represent standard errors of the mean;  $n = 5$  in each group. Roman numerals refer to order of presentation (first or second) of the set defined by variations in the respective spatial parameter—groove width (GW) or ridge width (RW).

of 8 subjects participated in this experiment, of whom 2 were left-handed and 6 were right-handed. For each set, training began with the dominant hand in 3 subjects, and the nondominant hand in 2 subjects. The data from all subjects who ran in this experiment were also used in Experiment 1, but the converse was not true; 3 subjects of Experiment 1 did not run in Experiment 2.<sup>1</sup>

### Results and Discussion

Since the results were similar for the contralateral index finger and the middle finger and not all subjects were tested on the middle finger, data were pooled across subsequently trained fingers, so that  $n$  was larger for these fingers.

Initial DLs were consistently and significantly ( $p = .008$ ) lower on subsequently trained fingers than on the first-trained finger (Figures 3 and 4). As in Experiment 1, the effect of grating set was significant ( $p = .04$ ) but not its interaction with order of finger trained ( $p = .34$ ).

The percentage decline in DL was significantly smaller ( $p = .02$ ) and the number of sessions required to attain it was significantly fewer ( $p = .001$ ) for subsequently trained fingers (Table 2), whereas grating set again did not significantly affect either dependent variable ( $p = .34$  and  $.12$ , respectively) and there was no significant interaction between grating set and the order in which fingers were tested ( $p = .96$  and  $.28$ , respectively). Again, the lack of significant effect of grating set on these measures justifies pooling the results of this experiment across grating sets.

Thus, practice effects transferred quite substantially between fingers (of either hand) tested sequentially with the same grating set. This was evidenced by the lower initial DLs and the smaller magnitude and faster development of learning effects (from lower initial values to comparable absolute end points; see Figure 4) on subsequently trained fingers than on the first-trained finger. In some cases, this transfer was complete; that is, the initial DL on a subsequently tested finger was comparable to the final DL on the first-trained finger. A similar result

was obtained in our preliminary experimental series with 1 subject for a grating set with GW varying cyclically along each comparison grating.

Tactile learning in this task, therefore, generalizes easily between fingers, unlike visual learning, which is highly location specific (Gilbert, 1994; Karni & Sagi, 1991; Ramachandran, 1976; Sagi & Tanne, 1994). It is remarkable that such transfer occurs for fingers of either hand. This implies that the neural basis of such generalization involves efficient inter- as well as intrahemispheric communication. Our data do not permit assessment of the relative efficiency of interhemispheric versus intrahemispheric transfer.

### General Discussion Experiments 1 and 2

Final DLs in this study averaged about 5%–10% of the baseline value (nominally 2.0 mm), which is comparable to that reported in an earlier study of grating discrimination where grating spatial period was varied by

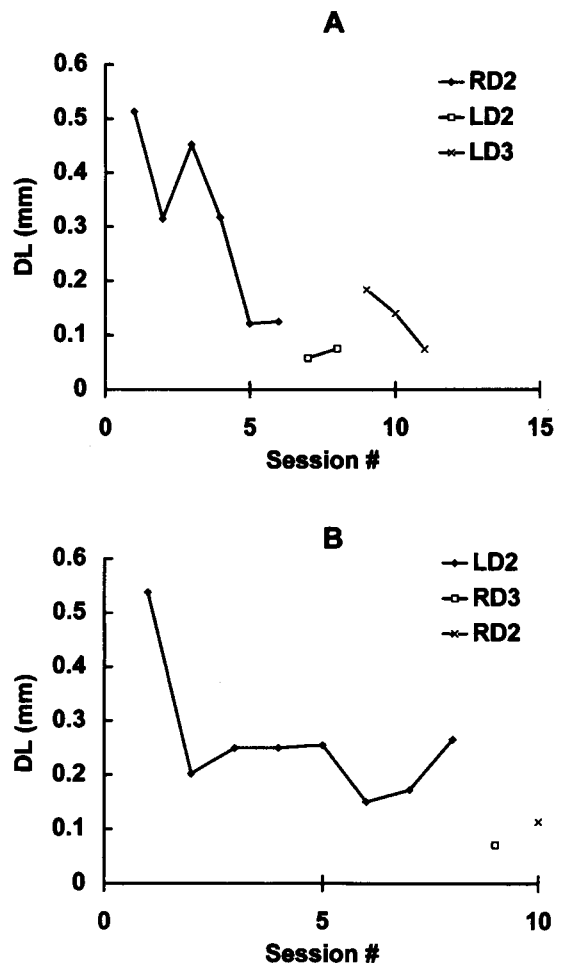


Figure 3. Difference limens (DLs) obtained for two representative individual subjects in successive sessions in Experiment 2, on the first-trained and subsequently trained fingers. (A) GW-varying set; (B) RW-varying set. L, left; R, right; D2, index finger; D3, middle finger; GW, groove width; RW, ridge width.

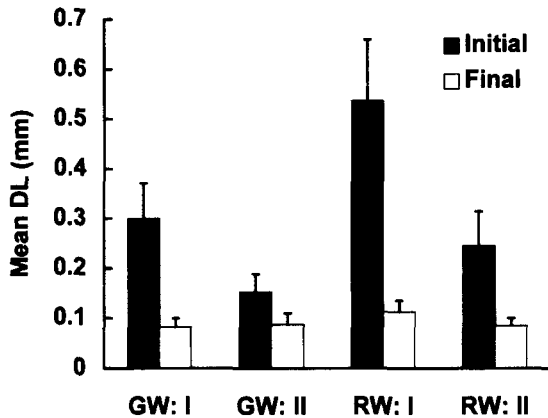


Figure 4. Mean initial and final difference limens (DLs) across subjects in Experiment 2. Bars represent standard errors of the mean. I, first-trained finger ( $n = 5$  for each set); II, subsequently trained fingers ( $n = 8$  for each set).

concomitant changes in GW and RW, the ratio of these two parameters being constant (Morley et al., 1983). Discrimination at initial as well as final levels was in the hyperacuity range—that is, finer than that expected by a spatial coding mechanism that depends on the receptor spacing of approximately a millimeter, and comparable to other measures of tactile hyperacuity (Loomis, 1979; Wheat, Goodwin, & Browning, 1995).

The finding of lower DLs for the GW-varying set compared to the RW-varying set is consistent with previous observations that changes in RW are more difficult to perceive than those in GW (Sathian et al., 1989; Sathian & Burton, 1991), that the peripheral neural representation of RW variation is not as rich as that of GW variation (Sathian et al., 1989; Goodwin et al., 1989) and that dot diameter affects roughness magnitude estimates and peripheral neural responses less effectively than dot spacing in the case of 2-D dot patterns (Connor et al., 1990). Close inspection of Figure 2 and Table 2 suggests further that the limited transfer of learning between sets in Experiment 1 may have been greater from the RW set to the GW set than vice versa. This could be due either to truly asymmetric transfer or to a ceiling effect on performance with the GW set. Although further analysis of these alternatives is not feasible, either is consistent with the greater difficulty of the RW set.

It is theoretically possible that miniscule variations in GW on the copies of the standard grating in the RW set (Table 1) could have actually detracted from performance with this set. This seems improbable, however, since these GW deviations of 0.03–0.04 mm from the GW on the standard were in the range of final DL for the GW set for only 2 of 10 subjects tested on this set, one of whom went on to achieve a final DL of less than the physically minimal  $\Delta$  for the RW set. Moreover, the training procedure adhered to the classic principle (Gibson, 1953) of progressing from easy to difficult discrimination within

each set, which would have served to maximize Gibsonian extraction of unique features for each set rather than focusing on much more minor cues that were irrelevant.

Although our study was not aimed at within-session learning effects, there were a number of occasions when one grating was presented in separate blocks in the same session. This provided an unplanned opportunity to screen for the occurrence of within-session learning by comparing the  $d'$  values thus obtained. Such an analysis revealed that  $d'$  values were sometimes higher and sometimes lower in the later block than in the earlier block. Overall, however, there was a clear trend for them to be higher. This trend did not dissipate after the first session, unlike previously reported in visual learning (Karni & Sagi, 1993). Although these results are no more than suggestive, they may bear further investigation to determine whether there is a true difference between the sensory systems or whether particulars of the experimental conditions account for these differing results.

To summarize, then, the major findings of the preceding experiments: learning effects in grating discrimination are partially specific to grating spatial parameters, showing only limited transfer to parameters other than the trained one, but transfer quite readily to other fingers, either the adjacent finger on the same hand or the homologous finger of the other hand. The former finding was not surprising, in view of the prior literature (Fiorentini & Berardi, 1980; Gilbert, 1994; Karni & Sagi, 1991; Ramachandran & Braddick, 1973; Sagi & Tanne, 1994), but the latter finding was quite unexpected, since previous visual studies have reported that location specificity characterizes perceptual learning (Ramachandran, 1976; Karni & Sagi, 1991; Gilbert, 1994; Sagi & Tanne, 1994). Does the difference in location specificity between studies of vision and our Experiment 2 reflect a genuine difference between the visual and tactile systems, or is it attributable to particulars of the experimental conditions? Experiment 3 was designed to address this question.

### EXPERIMENT 3

#### Improvement in Tactile Spatial Acuity

We wondered whether transfer of learning between fingers in the preceding experiment was peculiar to our paradigm, which involved active movement of the fingerpad over the grating, whereas previous studies reporting location specificity have used stimuli in the absence of movement of the receptor surface. A different grating conformation was therefore used in a test of tactile acuity devised by van Boven and Johnson (1994a, 1994b) and used previously by us (Sathian & Zangaladze, 1996).

#### Method

Details of the method used can be found in the reports just cited. Briefly, a set of eight gratings cut into plastic domes, with equal GW and RW (JVP Domes, Stoelting, Wood Dale, IL) was used. Groove widths were 0.35, 0.5, 0.75, 1.0, 1.2, 1.5, 2.0, and 3.0 mm. Adhesive tape applied to the nail immobilized the fin-

gerpad. Foam padding was used at potential pressure points. The gratings were statically impressed into the fingerpad for about a second, oriented either along the long axis of the finger or perpendicular to it, with vision excluded, following which subjects were asked to state the orientation.

The performance measure was the percentage of correct responses per block of 50 trials, since bias is not expected and does not occur under typical testing conditions in this task (van Boven & Johnson, 1994a). The discrimination threshold was taken as the value of GW (in millimeters) corresponding to 75% correct identification of grating orientation, by linear interpolation between the two values on either side of this threshold (except when performance was exactly 75% correct for a particular grating). The minimum GW of 0.35 mm was taken as the threshold when performance on this grating exceeded 75% correct. Relevant to this experiment, we have shown that spatial acuity as thus tested is bilaterally symmetric and does not differ among fingers, except for the fifth finger, which has lower acuity (Sathian & Zangaladze, 1996).

Recruitment of subjects proceeded as outlined for the previous experiments. The experimental design was as for Experiment 2, the objective here being to study whether practice-related improvement in spatial acuity is specific to the trained finger. Eight subjects, 6 right- and 2 left-handed, took part in this experiment. Five of them also took part in Experiments 1 and 2 (3 before and 2 after running in this experiment), and a 6th had previously run in the preliminary version of Experiment 1. Training began with the dominant hand in 4 subjects and the nondominant hand in the other 4 subjects. Perceptual learning and transfer were studied using the same kinds of measures as those described for Experiments 1 and 2.

## Results and Discussion

Once again, effects were similar for the contralateral index finger and the middle finger; hence data were pooled across subsequently trained fingers, so that  $n$  was larger for subsequently trained fingers. One subject dropped out after testing on the first finger: data from this subject were therefore available only for this finger.

Figure 5 shows data from a typical subject and Figure 6, from the subject pool, illustrating that initial acuity was lower on subsequently trained fingers than on the first-trained finger; the effect was of marginal significance ( $p = .066$ ). Practice effects in this task were relatively small and did not differ significantly between first- and subsequently trained fingers ( $p = .49$ ). However,

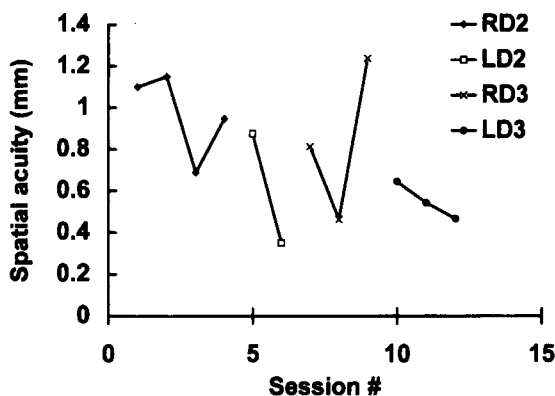


Figure 5. Spatial acuity for a representative subject in Experiment 3, in successive sessions on fingers tested sequentially. L, left; R, right; D2, index finger; D3, middle finger.

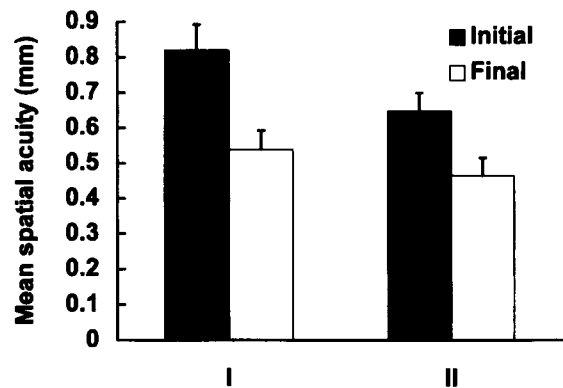


Figure 6. Mean initial and final spatial acuity across subjects in Experiment 3. Bars represent standard errors of the mean. I, first-trained finger ( $n = 8$ ); II, subsequently trained fingers ( $n = 15$ ).

they developed significantly faster (Table 2,  $p = .009$ ) on subsequently tested fingers of either hand than on the first-trained finger, reaching comparable final levels of acuity in either case (Figure 6).

Thus, the results of this experiment lend further support to the findings of Experiment 2. Interdigital transfer of tactile learning may therefore be a general phenomenon. Although we did not formally study this, initial discrimination ability in Experiment 3 did not seem to be affected by prior participation in Experiments 1 and 2, or vice versa, further emphasizing task specificity in tactile learning.

## GENERAL DISCUSSION

Our principal findings were that perceptual learning in the tactile system is quite as task specific as that in other sensory systems (Fiorentini & Berardi, 1980; Gilbert, 1994; Karni & Sagi, 1991; Ramachandran & Braddick, 1973; Sagi & Tanne, 1994), but it shows a unique propensity to transfer between fingers of either hand, in contrast to visual learning, which is quite location specific (Gilbert, 1994; Karni & Sagi, 1991; Ramachandran, 1976; Sagi & Tanne, 1994). This is particularly striking because location specificity in visual learning obtains in a wide variety of settings, including the perception of orientation, depth, motion, grating spatial phase, stereoacuity, and preattentive texture discrimination. It bears mention that the precise extent of transfer in each experiment in the present study was rather variable between subjects. This may reflect intrinsic variability in the process of transfer itself. Or, individual subjects might adopt variable strategies, some of which might lend themselves to more effective transfer.

Our failure to find digit specificity in tactile learning appears to contradict the only recent report on the topic (Recanzone, Jenkins, et al., 1992). However, we analyzed the data obtained on vibratory frequency discrimination for the single owl monkey in which this issue was exam-

ined in this study and found that, in fact, the results (Table 2) were quite comparable to ours. The DL (Hz) on the later tested digit was initially 40% lower (data not shown), declined by a smaller percentage, and stabilized sooner than on the first-trained digit, with comparable final values (Recanzone, Jenkins, et al., 1992). Thus, there was substantial transfer of practice-related improvement between adjacent fingers in their study, despite the authors' emphasis on specificity; in our Experiments 2 and 3, there was also a degree of residual specificity.

A recent abstracted report indicates that learning effects in spatial localization of vibratory stimuli on the finger also transfer between hands (Spengler et al., 1995). It appears, then, that the facility of transfer between fingers of one or both hands is the rule in tactile learning. However, in another recent abstracted report, intermanual transfer was not observed for vibratory amplitude discrimination on the palm (Bolanowski, Hall, Makous, & Merzenich, 1995), consistent with the location specificity of visual learning (Gilbert, 1994; Karni & Sagi, 1991; Ramachandran, 1976; Sagi & Tanne, 1994). A further complication is presented by early reports suggesting that practice effects on two-point discrimination on the forearm transfer to homologous areas contralaterally (Dresslar, 1895; Mukherjee, 1933) but not surrounding areas (Dresslar, 1895). It is difficult to evaluate these early reports in view of the small numbers of subjects (2 subjects in each study) and the generally low reliability of the two-point discrimination task (van Boven & Johnson, 1994a, 1994b).

One explanation that would reconcile at least the recent findings is that sensory information originating in the fingers is processed in a fundamentally different manner from that arising elsewhere on the hand (Merzenich et al., 1983) or in the retina. Alternatively, other factors, such as the nature of sensory information being processed or the requirement for attention (Sagi & Tanne, 1994), whether spatial (O'Toole & Kersten, 1992) or quantitative (Spitzer, Desimone, & Moran, 1988), may account for these intertask differences. In this context, it is interesting that practice effects in the acuity task are small compared with those in grating discrimination, which can be considered a hyperacuity task. This raises the following general question: Are hyperacuity tasks (McKee & Westheimer, 1978) prone to show greater degrees of perceptual learning than are simple acuity tasks?

Perhaps the high propensity for interdigital transfer of tactile learning is related to concomitant use of multiple fingers in tactile sensing and the ability, under some conditions, to divide attention among multiple fingers (Sathian & Burton, 1991; Whang, Burton, & Shulman, 1991). If the locus of perceptual learning indeed is in primary sensory cortex, as suggested in vision (Gilbert, 1994; Karni & Sagi, 1991), interdigit transfer of learning must depend on cortico-cortical and callosal connections between the representations of individual digits. Within primary somatosensory cortex (SI), callosal connections in the hand representation are extremely sparse in area 3b, but relatively denser in areas 1 and 2 (Killackey, Gould,

Cusick, Pons, & Kaas, 1983). Correspondingly, multi-digit receptive fields are not generally present in area 3b (Pons, Wall, Garraghty, Cusick, & Kaas, 1987). This line of reasoning suggests that area 3b is unlikely to be the sole site of learning effects: more posterior parts of SI (areas 1 and 2) could be involved.

However, other findings dictate a caveat to the suggestion above. Multidigit receptive fields occur in area 3b under unusual circumstances such as following surgical fusion of digits (Allard, Clark, Jenkins, & Merzenich, 1991) or prolonged multidigit stimulation (Wang, Merzenich, Sameshima, & Jenkins, 1995). Further, tactile stimuli can be perceptually remapped onto phantom digits (Ramachandran, 1993) and the hand contralateral to an amputated one (Ramachandran, 1995). Corresponding alterations in somatotopic maps have been described (Calford & Tweedale, 1990; Merzenich et al., 1984). It is thought that unmasking or reorganizing of subliminal inputs from adjacent or contralateral digits to the zone where a particular digit is represented in area 3b may mediate these phenomena. Such synaptic processes in area 3b could well underlie our own observations in this report.

Alternatively, tactile learning may depend partly or wholly on processes occurring in other cortical areas. The second somatosensory cortex (SII), in the parietal operculum, is a higher order area (Burton, Sathian, & Dian-Hua, 1990; Pons, Garraghty, Friedman, & Mishkin, 1987) that has been implicated in tactile learning on the basis of lesion studies (Murray & Mishkin, 1984; Ridley & Ettlinger, 1978). Potential neural substrates consistent with interdigital transfer include the profuse callosal connections of SII (Manzoni, Barbaresi, & Conti, 1984) and the commonly encountered multidigit and bilateral receptive fields in parietal opercular cortical zones (Robinson & Burton, 1980a, 1980b). Certainly, candidate areas are not necessarily restricted to those mentioned here. Planned functional neuroimaging and neurophysiological studies are likely to provide further insight into the localization and nature of the underlying neural processes.

## REFERENCES

- ALLARD, T., CLARK, S. A., JENKINS, W. M., & MERZENICH, M. M. (1991). Reorganization of somatosensory area 3b representations in adult owl monkeys after digital syndactyly. *Journal of Neurophysiology*, **66**, 1048-1058.
- BOLANOWSKI, S. J., HALL, K. L., MAKOUS, J. C., & MERZENICH, M. M. (1995). Intensity discrimination of vibratory stimuli can be improved by training. *Society for Neuroscience Abstracts*, **21**, 565.18.
- BURTON, H., SATHIAN, K., & DIAN-HUA, S. (1990). Altered responses to cutaneous stimuli in the second somatosensory cortex following lesions of the postcentral gyrus in infant and juvenile macaques. *Journal of Comparative Neurology*, **291**, 395-414.
- CALFORD, M. B., & TWEEDALE, R. (1990). Interhemispheric transfer of plasticity in the cerebral cortex. *Science*, **249**, 805-807.
- CONNOR, C. E., HSIAO, S. S., PHILLIPS, J. R., & JOHNSON, K. O. (1990). Tactile roughness: Neural codes that account for psychophysical magnitude estimates. *Journal of Neuroscience*, **10**, 3823-3836.
- CRAIG, J. C. (1988). The role of experience in tactual pattern perception: A preliminary report. *International Journal of Rehabilitation Research*, **11**, 167-183.
- DARIAN-SMITH, I. (1984). The sense of touch: Performance and peripheral neural processes. In I. Darian-Smith (Ed.), *Handbook of*



- physiology—*The nervous system: Vol. III. Sensory processes* (pp. 739-788). Bethesda, MD: American Physiological Society.
- DARIAN-SMITH, I., & OKE, L. E. (1980). Peripheral neural representation of the spatial frequency of a grating moving across the monkey's finger pad. *Journal of Physiology*, **309**, 117-133.
- DRESSLAR, F. B. (1895). Studies in the psychology of touch. *American Journal of Psychology*, **6**, 313-368.
- EPSTEIN, W., HUGHES, B., SCHNEIDER, S. L., & BACH-Y-RITA, P. (1989). Perceptual learning of spatiotemporal events: Evidence from an unfamiliar modality. *Journal of Experimental Psychology: Human Perception & Performance*, **15**, 28-44.
- FIORENTINI, A., & BERARDI, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, **287**, 43-44.
- GIBSON, E. J. (1953). Improvement in perceptual judgments as a function of controlled practice or training. *Psychological Bulletin*, **50**, 401-431.
- GIBSON, E. J. (1969). *Principles of perceptual learning and development*. New York: Meredith.
- GILBERT, C. D. (1994). Early perceptual learning. *Proceedings of the National Academy of Sciences*, **91**, 1195-1197.
- GOODWIN, A. W., JOHN, K. T., SATHIAN, K., & DARIAN-SMITH, I. (1989). Spatial and temporal factors determining afferent fiber responses to a grating moving sinusoidally over the monkey's fingerpad. *Journal of Neuroscience*, **9**, 1280-1293.
- GOODWIN, A. W., MORLEY, J. W., CLARKE, C., LUMAKSANA, B., & DARIAN-SMITH, I. (1985). A stimulator for moving textured surfaces sinusoidally across the skin. *Journal of Neuroscience Methods*, **14**, 121-125.
- HELLER, M. A. (1989). Texture perception in sighted and blind observers. *Perception & Psychophysics*, **45**, 49-54.
- KAAS, J. H. (1991). Plasticity of sensory and motor maps in adult mammals. *Annual Review of Neuroscience*, **14**, 137-167.
- KARNI, A., & SAGI, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences*, **88**, 4966-4970.
- KARNI, A., & SAGI, D. (1993). The time course of learning a visual skill. *Nature*, **365**, 250-252.
- KILLACKEY, H. P., GOULD, H. J., CUSICK, C. G., PONS, T. P., & KAAS, J. H. (1983). The relation of corpus callosum connections to architectonic fields and body surface maps in sensorimotor cortex of New and Old World monkeys. *Journal of Comparative Neurology*, **219**, 384-419.
- KLATZKY, R. L., LEDERMAN, S., & REED, C. (1987). There's more to touch than meets the eye: The salience of object attributes for haptics with and without vision. *Journal of Experimental Psychology: General*, **116**, 356-369.
- LAMB, G. D. (1983). Tactile discrimination of textured surfaces: Psychophysical performance measurements in humans. *Journal of Physiology*, **338**, 551-565.
- LEDERMAN, S. J., & TAYLOR, M. M. (1972). Fingertip force, surface geometry, and the perception of roughness by active touch. *Perception & Psychophysics*, **12**, 401-408.
- LOOMIS, J. M. (1979). An investigation of tactile hyperacuity. *Sensory Processes*, **3**, 289-302.
- MANZONI, T., BARBARESI, P., & CONTI, F. (1984). Callosal mechanism for the interhemispheric transfer of hand somatosensory information in the monkey. *Behavioral Brain Research*, **11**, 155-170.
- McKEE, S. P., & WESTHEIMER, G. (1978). Improvement in vernier acuity with practice. *Perception & Psychophysics*, **24**, 258-262.
- MERZENICH, M. M., KAAS, J. H., WALL, J. T., SUR, M., NELSON, R. J., & FELLEMAN, D. J. (1983). Progression of change following median nerve section in the cortical representation of the hand in areas 3b and 1 in adult owl and squirrel monkeys. *Neuroscience*, **10**, 639-665.
- MERZENICH, M. M., NELSON, R. J., STRYKER, M. P., CYNADER, M. S., SCHOPPMANN, A., & ZOOK, J. M. (1984). Somatosensory cortical map changes following digit amputation in adult monkeys. *Journal of Comparative Neurology*, **224**, 591-605.
- MERZENICH, M. M., & SAMESHIMA, K. (1993). Cortical plasticity and memory. *Current Opinion in Neurobiology*, **3**, 187-196.
- MORLEY, J. W., GOODWIN, A. W., & DARIAN-SMITH, I. (1983). Tactile discrimination of gratings. *Experimental Brain Research*, **49**, 291-299.
- MUKHERJEE, K. C. (1933). The duration of cutaneous sensation (I) and the improvement of its sensible discrimination by practice (II). *Journal of Experimental Psychology*, **16**, 339-342.
- MURRAY, E. A., & MISHKIN, M. (1984). Relative contributions of SII and area 5 to tactile discrimination in monkeys. *Behavioral Brain Research*, **11**, 67-83.
- O'TOOLE, A., & KERSTEN, D. J. (1992). Learning to see random-dot stereograms. *Perception*, **21**, 227-243.
- PONS, T. P., GARRAGHTY, P. E., FRIEDMAN, D. P., & MISHKIN, M. (1987). Physiological evidence for serial processing in somatosensory cortex. *Science*, **237**, 417-420.
- PONS, T. P., WALL, J. T., GARRAGHTY, P. E., CUSICK, C. G., & KAAS, J. H. (1987). Consistent features of the representation of the hand in area 3b of macaque monkeys. *Somatosensory Research*, **4**, 309-331.
- RAMACHANDRAN, V. S. (1976). Learning-like phenomena in stereopsis. *Nature*, **262**, 392-394.
- RAMACHANDRAN, V. S. (1993). Behavioral and magnetoencephalographic correlates of plasticity in the adult human brain. *Proceedings of the National Academy of Sciences*, **90**, 10413-10420.
- RAMACHANDRAN, V. S. (1995). Touching the phantom limb. *Nature*, **377**, 489-490.
- RAMACHANDRAN, V. S., & BRADDICK, O. (1973). Orientation-specific learning in stereopsis. *Perception*, **2**, 371-376.
- RECANZONE, G. H., JENKINS, W. M., HRADEK, G. T., & MERZENICH, M. M. (1992). Progressive improvement in discriminative abilities in adult owl monkeys performing a tactile frequency discrimination task. *Journal of Neurophysiology*, **67**, 1015-1030.
- RECANZONE, G. H., MERZENICH, M. M., & JENKINS, W. M. (1992). Frequency discrimination training engaging a restricted skin surface results in an emergence of a cutaneous response zone in cortical area 3a. *Journal of Neurophysiology*, **67**, 1057-1070.
- RECANZONE, G. H., MERZENICH, M. M., JENKINS, W. M., GRAJSKI, K. A., & DINSE, H. R. (1992). Topographic reorganization of the hand representation in cortical area 3b of owl monkeys trained in a frequency-discrimination task. *Journal of Neurophysiology*, **67**, 1031-1056.
- RECANZONE, G. H., MERZENICH, M. M., & SCHREINER, C. E. (1992). Changes in the distributed temporal response properties of SI cortical neurons reflect improvements in performance on a temporally based tactile discrimination task. *Journal of Neurophysiology*, **67**, 1071-1091.
- RECANZONE, G. H., SCHREINER, C. E., & MERZENICH, M. M. (1993). Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *Journal of Neuroscience*, **13**, 87-103.
- RIDLEY, R. M., & ETTLINGER, G. (1978). Further evidence of impaired tactile learning after removals of the second somatic sensory projection cortex (SII) in the monkey. *Experimental Brain Research*, **31**, 475-488.
- ROBINSON, C. J., & BURTON, H. (1980a). Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis*. *Journal of Comparative Neurology*, **192**, 69-92.
- ROBINSON, C. J., & BURTON, H. (1980b). Somatotopographic organization in the second somatosensory area of *M. fascicularis*. *Journal of Comparative Neurology*, **192**, 43-67.
- SAGI, D., & TANNE, D. (1994). Perceptual learning: Learning to see. *Current Opinion in Neurobiology*, **4**, 195-199.
- SATHIAN, K. (1989). Tactile sensing of surface features. *Trends in Neurosciences*, **12**, 513-519.
- SATHIAN, K., & BURTON, H. (1991). The role of spatially selective attention in the tactile perception of texture. *Perception & Psychophysics*, **50**, 237-248.
- SATHIAN, K., GOODWIN, A. W., JOHN, K. T., & DARIAN-SMITH, I. (1989). Perceived roughness of a grating: Correlation with responses of mechanoreceptive afferents innervating the monkey's fingerpad. *Journal of Neuroscience*, **9**, 1273-1279.
- SATHIAN, K., & ZANGALADZE, A. (1995). Perceptual learning in tactile texture discrimination. *Society for Neuroscience Abstracts*, **21**, 50.19

## NOTE

- SATHIAN, K., & ZANGALADZE, A. (1996). Tactile spatial acuity at the human fingertip and lip: Bilateral symmetry and inter-digit variability. *Neurology*, **46**, 1464-1466.
- SHIU, L.-P., & PASHLER, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, **52**, 582-588.
- SPENGLER, E., ROBERTS, T., ROWLEY, H., WANG, X., WRIGHT, B., & MERZENICH, M. (1995). Tactile training effects revealed by functional imaging in the human cortex. *Society for Neuroscience Abstracts*, **21**, 52.6.
- SPITZER, H., DESIMONE, R., & MORAN, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science*, **240**, 338-340.
- VAN BOVEN, R. W., & JOHNSON, K. O. (1994a). The limit of tactile spatial resolution in humans: Grating orientation discrimination at the lip, tongue and finger. *Neurology*, **44**, 2361-2366.
- VAN BOVEN, R. W., & JOHNSON, K. O. (1994b). A psychophysical study of the mechanisms of sensory recovery following nerve injury in humans. *Brain*, **117**, 149-167.
- WANG, X., MERZENICH, M. M., SAMESHIMA, K., & JENKINS, W. M. (1995). Remodelling of hand representation in adult cortex determined by timing of tactile stimulation. *Nature*, **378**, 71-75.
- WEINBERGER, N. M. (1995). Dynamic regulation of receptive fields and maps in the adult sensory cortex. *Annual Review of Neuroscience*, **18**, 129-158.
- WHANG, K. C., BURTON, H., & SHULMAN, G. L. (1991). Selective attention in vibrotactile tasks: Detecting the presence and absence of amplitude change. *Perception & Psychophysics*, **50**, 157-165.
- WHEAT, H. E., GOODWIN, A. W., & BROWNING, A. S. (1995). Tactile resolution: Peripheral neural mechanisms underlying the human capacity to determine positions of objects contacting the fingerpad. *Journal of Neuroscience*, **15**, 5582-5595.

1. It is unlikely that participation in both Experiments 1 and 2 by most of our subjects materially affected the results. Four subjects ran in Experiment 1 first, completing both sets on the first-trained index finger. Subsequent testing of other fingers in Experiment 2 used only the last-tested set. Three other subjects of Experiment 1 did not run in Experiment 2. Two subjects participated in both experiments contemporaneously; that is, after initial training with one set on one index finger, sessions were divided into two parts, in one of which they were presented the second set on the same finger while the original set was used on other fingers in the other part of the same session. One subject was first tested on multiple fingers with the same grating set and then proceeded to be tested on multiple fingers with the other set. None of these variations in sequence seemed to affect the likelihood of transfer. The considerable specificity of learning effects in Experiment 1 "insulated" against at least major leak-through of learning effects between sets, while the general rapidity with which learning effects plateaued in Experiment 2 did not afford subjects with unduly prolonged opportunities to learn. Obviously, further experiments with larger numbers of subjects and either a "wall" between experiments or direct comparison of between-set and between-finger transfer in the same subject pool would be ideal. However, in view of the clear differences we found in transfer of learning between Experiments 1 and 2 (which, further, were consistent with our preliminary experiments with another paradigm), we do not feel these to be warranted at the present time.

(Manuscript received January 4, 1996;  
revision accepted for publication March 25, 1996.)