

The Topography of Tactile Learning in Humans

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The spatial distribution of learned information within a sensory system can shed light on the brain mechanisms of sensory–perceptual learning. It has been argued that tactile memories are stored within a somatotopic framework in monkeys and rats but within a widely distributed network in humans. We have performed experiments to reexamine the spread of tactile learning across the fingertips. In all experiments, subjects were trained to use one fingertip to discriminate between two stimuli. Experiment 1 required identification of vibration frequency, experiment 2 punctate pressure, and experiment 3 surface roughness. After learning to identify the stimuli reliably, subjects were tested with the trained fingertip, its first and second neighbors on the same hand, and the three corresponding fingertips on the opposite hand. As expected, for all stimulus types, subjects showed retention of learning with the trained fingertip. How-

ever, the transfer beyond the trained fingertip varied according to the stimulus type. For vibration, learning did not transfer to other fingertips. For both pressure and roughness stimuli, there was limited transfer, dictated by topographic distance; subjects performed well with the first neighbor of the trained finger and with the finger symmetrically opposite the trained one. These results indicate that tactile learning is organized within a somatotopic framework, reconciling the findings in humans with those in other species. The differential distribution of tactile memory according to stimulus type suggests that the information is stored in stimulus-specific somatosensory cortical fields, each characterized by a unique receptive field organization, feature selectivity, and callosal connectivity.

Key words: somatosensory; cortex; vibration discrimination; von Frey; roughness discrimination; plasticity

There are two main views concerning the role of sensory cortex in perceptual learning and memory, one in which processed sensory information is relayed to “late” cortical regions that subserve information storage, and a second in which “early” sensory processing regions themselves contribute to information storage. Investigating how learned information is spatially distributed in relation to the sensory organ itself can help distinguish between these hypotheses. Specifically, subjects that have learned a task using a restricted part of the sensory apparatus can be later tested using other parts of the sensory apparatus. If the learned information resides in late areas whose organization does not conserve the topographic arrangement of the sensory apparatus, then it will be accessible independently of the part of the receptor organ used during testing. In contrast, if the learned information resides in early cortical areas whose organization conserves the topographic arrangement of the sensory apparatus, then its accessibility will be determined by the spatial relationship between the receptors used during learning versus testing.

Using this strategy, we observed patterns of tactile learning in rats that suggest that primary somatosensory cortical topography plays an essential role in shaping the distribution of learned information (Harris et al., 1999; Harris and Diamond, 2000). Specifically, having trained rats to use a single whisker in a goal-detection task, we found that the extent to which learning transferred across whisker positions was precisely dictated by the distance between the trained and tested whiskers and by the

degree of overlap between the representations of those whiskers in barrel cortex (Harris et al., 1999).

However, the view that tactile learning is topographically distributed is not uniformly accepted (Sathian and Zangaladze, 1997, 1998; Spengler et al., 1997; Nagarajan et al., 1998). Therefore, the first goal of the present experiments was to investigate whether the topographic learning principle discovered in rats would generalize to humans. The second goal was to gain insight into how the functional organization of the sensory system might underlie the principle. Because specific types of tactile stimuli are processed in specialized cortical areas, each possessing a unique topographic organization (Kaas, 1993), we expected that the topographic distribution of learning in humans would vary for different classes of tactile stimulus. Thus, we compared the transfer of a learned discriminative ability for three tactile stimuli: low-frequency vibration, punctate pressure delivered by von Frey hairs, and roughness. These were chosen because much is known about the peripheral and central mechanisms involved in processing these stimuli (Johnson and Hsiao, 1992). In each experiment, subjects were trained to recognize two stimuli using a single “trained” finger (T) and were then tested with that finger as well as its immediate (I_1) and second (I_2) ipsilateral neighbors (Fig. 1). We also examined learning transfer to the three corresponding fingers on the contralateral hand (C, C_1 , and C_2). In all three experiments, the learned information was somatotopically distributed, and the learning distributions were stimulus-specific. These observations support the idea that topographically organized regions of sensory cortex have an essential role in information storage.

MATERIALS AND METHODS

Subjects. There were eight subjects in each experiment: four males and four females in experiment 1 (vibration); five males and three females in experiment 2 (punctate pressure); and three males and five females in

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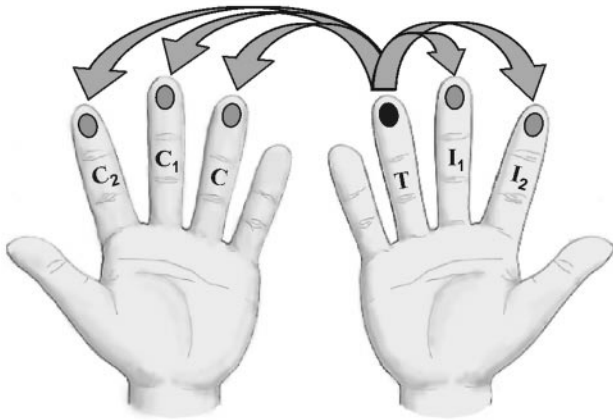


Figure 1. Summary of the experimental design. Subjects were trained on a tactile discrimination using one fingertip (*T*; the fourth digit of the right hand in this example). They were then tested with that finger, as well as its first and second neighbors (*I*₁ and *I*₂), and the corresponding three fingers on the opposite hand (*C*, *C*₁, and *C*₂).

experiment 3 (roughness). All were right-handed and ranged in age from 21 to 52 years. There were five subjects common to experiments 1 and 2. Recruitment of subjects and experimental procedures were conducted in accordance with the *Declaration of Helsinki*.

Materials. The vibrotactile stimulus was delivered by a piezoelectric wafer (Morgan Matroc, Bedford, OH) driven by 20 V pulses controlled by a computer running Labview (National Instruments, Austin, TX). The punctate pressure stimuli were applied using von Frey hairs (Semmes-Weinstein Monofilaments, Stoelting, IL). The two filaments were 0.254 and 0.305 mm in diameter, providing forces of 1.48 and 2.04 gm, respectively. Commercially produced garnet sandpaper (Norton Abrasives, Hamilton, Canada) was used in the roughness discrimination protocol of experiment 3. The sandpaper surfaces were as follows. The rougher surface (grit grade “40-D”) had a mean of 2.1 grains per square millimeter with the average diameter of each grain being 470 μ m; the smoother (grade “60-D”) had 3.9 grains per square millimeter, each of 375 μ m in diameter.

Procedure. Subjects were trained and tested in a single session. The duration of the session varied between 1 and 2.5 hr depending on how quickly individual subjects reached criterion during training.

Training. For each subject, one finger was selected for training. The specific finger differed for each subject in a given experiment, such that each of the eight fingers (excluding the thumbs) served as a trained finger. This was done to ensure that any topographic pattern observed on testing was not confounded by potential differences in sensitivity between specific fingers. The experiments proceeded as a continuous sequence of trials in which one of two stimuli was delivered to the training finger; the subject’s task was to name which of the two stimuli had been presented (subjects could choose their own labels for the stimuli, and the most common ones were “fast” or “slow” vibration, “hard” or “soft” pressure, and “rough” or “smooth” surface). The first 20 trials were used to collect baseline data of the subject’s naïve accuracy. These data served for comparison against subsequent test performance for all fingers. After collection of baseline data, every subsequent trial included feedback to facilitate learning.

Testing. For each experiment, the test phase commenced at completion of training. On each test trial, subjects had to judge which of the two stimuli had been presented. The test was administered in groups of six trials: on each trial, the stimulus was applied to a different finger (*T*, *I*₁, *I*₂, *C*, *C*₁, and *C*₂). The sequence of stimulus sites was random and varied from one group of six trials to the next. This testing procedure ensured that there was no systematic effect of test order across fingers. The specific stimulus delivered on a given trial was selected at random, with the condition that each of the two stimuli was delivered an equal number of times across the test trials.

Experiment 1 (vibration). At the beginning of each trial, the subjects were instructed to rest their fingerpad on the piezoelectric wafer. The vibration (a square wave of 80 μ m amplitude) was then delivered for 1 sec, either at the low (9 Hz) or high (10 Hz) frequency. During training, three of the subjects received between 80 and 120 trials with an easier

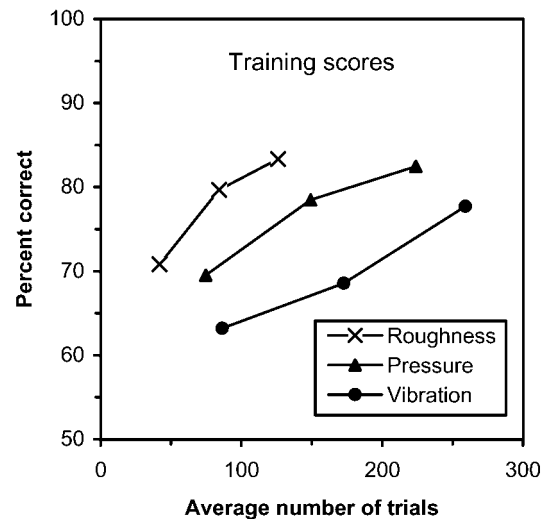


Figure 2. Time course of learning for vibration (experiment 1), punctate pressure (experiment 2), and roughness (experiment 3) discriminations. Each subject’s training session was divided into three segments with equal numbers of trials. The *three data points* represent the average number of trials in each segment (*x*-axis) and the percent of correct trials in each segment (*y*-axis).

discrimination (8 vs 10 Hz) before proceeding to the standard 9 versus 10 Hz discrimination. For each subject, training was stopped when they reached a criterion of at least 32 correct responses of 40 trials (80% accuracy). The test phase consisted of 120 trials, comprising 20 trials for each of the six fingers tested.

Experiment 2 (punctate pressure). Subjects were blindfolded and sat with their palms facing up. To ensure that stimuli were always applied to the same site, a small black dot was in the center of the fingerprint for each of the six fingers tested. On each trial, the experimenter touched the marked location with one of the two filaments, and the subject stated whether this was the “harder” or “softer” of the two. Training was stopped when subject reached a criterion of at least 32 correct responses of 40 trials (80% accuracy). Like experiment 1, the test phase consisted of 120 trials, comprising 20 trials for each of the six fingers.

Experiment 3 (roughness). Subjects were blindfolded and rested their wrists on a desktop, fingers elevated. On each trial, the experimenter placed one of two surfaces under the selected finger and asked the subject to touch the surface. Subjects were instructed not to move their fingers across the surface. Training was stopped when subjects reached a criterion of 12 consecutive correct trials. Discrimination learning proceeded faster in this experiment than in the previous ones. Therefore, we reduced the number of test trials to avoid the potential confound that would occur if subjects began to learn the discrimination *de novo* with their untrained fingers. The test phase consisted of 72 trials, comprising 12 trials for each of the six fingers.

Statistical analyses. For each experiment, the scores for each of the six fingers tested were compared with the baseline performance of the trained finger using a paired Student’s *t* test conducted on the pooled data from all eight subjects. Test performance for the trained finger was also compared against test performance of each of the other five fingers using a paired Student’s *t* test on the same pooled data. This within-subjects analysis ensured that between-subjects variability did not influence the results. For the 11 comparisons, the experiment-wise error rate was controlled using a Bonferroni adjustment, whereby α (set at 0.05) was divided by 11. Thus, only differences for which $p < 0.0045$ were deemed significant.

RESULTS

Learning of the discrimination task

In each experiment, baseline performance was marginally better than chance (mean scores varied between 61.9 and 66.7%). Because they were trained to criterion, each subject received a different number of training trials. Therefore, to analyze their

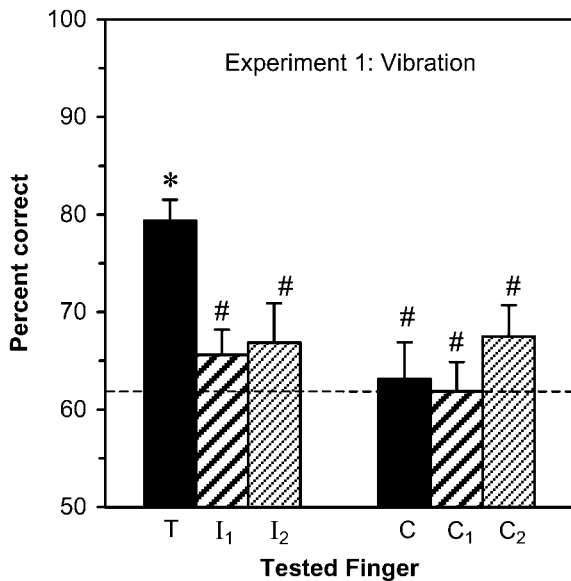


Figure 3. The mean percent correct with each finger tested for vibration discrimination in experiment 1. * indicates performance significantly above baseline (shown by broken line); # indicates performance significantly below that for finger T (all p values < 0.0045); error bars represent SEMs.

performance across training, we grouped the scores for each subject into three blocks. Figure 2 plots the average number of trials per block (i.e., the average total number of trials divided by three) against the average percent of correct responses for each of the three blocks. Some task-related differences in the course of learning can be discerned. For roughness discrimination, subjects showed a rapid rate of improvement and reached criterion after 126 training trials, on average. For vibration discrimination, subjects showed a more gradual rate of improvement and therefore required more trials (262, on average) to reach criterion. For punctate pressure discrimination, the rate of improvement and the number of trials to criterion (221, on average) were intermediate.

Test performance

The principal result is that test performance varied across fingers in an orderly manner, and the spatial pattern of performance varied according to the type of stimulus (Figs. 3–5). For the vibratory stimulus (Fig. 3, experiment 1), accuracy was high for test trials using the trained finger but was low for all other fingers. Statistical analysis revealed that performance with the trained finger T was significantly better than baseline ($p = 0.0038$). In contrast, no other finger yielded performance significantly different from baseline ($p = 0.142$ for I_1 ; $p = 0.187$ for I_2 ; $p = 0.422$ for C; $p = 0.5$ for C_1 ; and $p = 0.134$ for C_2). Moreover, the subjects' test performance with T was better than their test performance with all other fingers ($p = 0.0015$ for I_1 ; $p = 0.0026$ for I_2 ; $p = 0.0014$ for C; $p = 0.0004$ for C_1 ; and $p = 0.0026$ for C_2). Thus, if there was any transfer of learning from the trained finger to any other finger, it must have been incomplete.

Learning was more widely distributed for the punctate pressure stimulus (Fig. 4, experiment 2). In addition to the trained finger (T), accuracy was high for the first neighbor (I_1) and for the contralateral finger opposite the trained one (C). Accuracy was much lower for the other three fingers. Statistical analysis confirmed that there was a significant difference between baseline

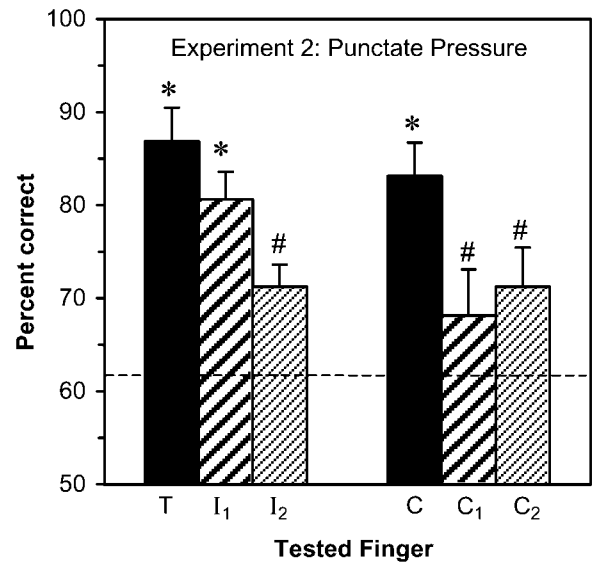


Figure 4. The mean percent correct with each finger tested for punctate pressure discrimination in experiment 2. * indicates performance significantly above baseline (shown by broken line); # indicates performance significantly below that for finger T (all p values < 0.0045); error bars represent SEMs.

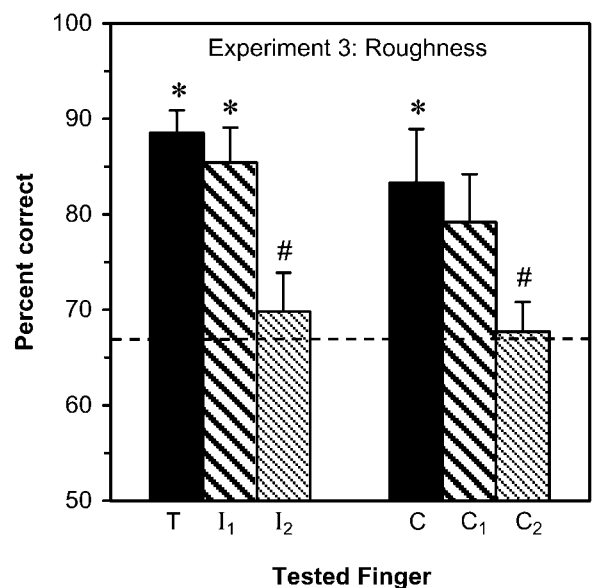


Figure 5. The mean percent correct with each finger tested for roughness discrimination in experiment 3. * indicates performance significantly above baseline (shown by broken line); # indicates performance significantly below that for finger T (all p values < 0.0045); error bars represent SEMs.

and test performance for T ($p = 0.00003$), I_1 ($p = 0.003$), and C ($p = 0.0001$). Test performance with these latter two fingers did not differ significantly from that of the trained finger ($p = 0.053$ and 0.230 , respectively). In contrast, there was no significant difference between baseline and test performance for I_2 ($p = 0.035$), C_1 ($p = 0.146$), or C_2 ($p = 0.013$). Although the comparisons to baseline for I_2 and C_2 could be deemed significant with a less strict criterion, it is important that test performance for both these fingers, as well as for C_1 , was significantly different from that

of finger T ($p = 0.0036$ for I_2 ; $p = 0.0005$ for C_1 ; and $p = 0.0045$ for C_2). Thus, any transfer of learning from the trained finger to these fingers must have been incomplete.

For roughness discrimination (Fig. 5, experiment 3), the distribution of learning was similar to that for punctate pressure discrimination. There were significant differences between baseline performance and test performance for the trained finger T ($p = 0.0016$), its first neighbor I_1 ($p = 0.0033$), and the corresponding finger on the other hand C ($p = 0.0006$). These latter two fingers were not significantly different from T ($p > 0.18$ for both comparisons), confirming that learning did transfer from T. In contrast, there were no significant differences between baseline and test performance for I_2 ($p = 0.28$) and C_2 ($p = 0.40$); moreover, these fingers differed significantly from the trained finger T ($p = 0.0013$ for I_2 ; $p = 0.0003$ for C_2), confirming that learning did not transfer to these fingers. The performance with finger C_1 was ambiguous because it was not significantly different from baseline ($p = 0.06$), suggesting a failure of transfer, yet with the strict criteria applied to these data it was not significantly different from the performance with finger T ($p = 0.013$).

DISCUSSION

Principal findings

This study has shown that, under the present experimental conditions, tactile learning in humans is topographically distributed and that the precise pattern of the distribution depends on the features of the acquired information. When subjects learned to distinguish vibration frequencies, the improvement in performance was confined to the trained fingertip. Conversely, when they learned to distinguish punctate stimuli of different force, or surfaces of different roughness, the improvement in performance showed a limited range of transfer: to the first neighbor of the trained finger (I_1) and to the finger symmetrically opposite the trained one (C), but not to the second neighbors of either the trained finger (I_2) or the corresponding finger on the other hand (C_2). These differences between stimulus types were not related in any simple way to the difficulty of the discriminations, because the rate of learning of the pressure discrimination was similar to that for vibration, yet the learning transfer pattern for pressure was similar to that for roughness.

Several previous studies have failed to detect a topography for tactile learning; when subjects were trained with one finger to discriminate between two tactile stimuli, their learned ability readily transferred to all tested sites (Sathian and Zangaladze, 1997, 1998; Spengler et al., 1997). These observations were taken as “complete transfer,” implying that the learning was not topographically distributed. However, most of these studies only tested for transfer to the neighboring finger or the corresponding finger on the opposite hand. Our results show that a true topography of tactile learning can be uncovered when a more widely distributed range of sites is tested. In this, the present findings are consistent with numerous studies reporting a retinotopic distribution for visual learning (Karni and Sagi, 1991; Fahle, 1994; Ahissar and Hochstein, 1996; Schoups and Orban, 1996; Dill and Fahle, 1997, 1998) and so resolve the apparent discrepancy between visual and tactile learning by showing that both can reside within a spatially constrained framework.

The finding that a tactile memory trace is distributed with a spatial gradient, rather than uniformly, can be most simply explained by proposing that the learned information is stored within early sensory cortical areas, because these areas are topographically organized (for similar reasoning with respect to visual learn-

ing, see Karni and Sagi, 1991; Fahle, 1994). Not only is tactile learning topographically distributed, but we have shown that its exact spatial pattern depends on the specific features of the stimuli. We suggest that these different spatial transfer patterns may relate to differences in the neural mechanisms for processing the stimulus. The neural pathways that encode vibration, on the one hand, and pressure and roughness, on the other, respect a basic segregation; vibration is encoded by peripheral and central neurons with rapidly adapting properties, whereas pressure and roughness are encoded by slowly adapting neurons (Johnson and Hsiao, 1992). In the following sections, we use the detailed patterns of transfer to generate hypotheses concerning which neural substrates subserve the stored information. However, in arguing for the critical contribution of a given cortical area, we do not intend to rule out the involvement of other cortical areas. The discussion is based on data from nonhuman primates (except where noted); we assume that somatosensory processing in humans is organized similarly.

Vibration discrimination

Learning of the vibration discrimination did not transfer to any other finger. This topographic specificity rules out a more cognitive strategy for encoding the stimulus, such as counting the number of deflections, because such a strategy should show complete transfer across fingers. As a neural locus for the encoded information, we therefore seek to identify a somatosensory cortical field in which neurons (1) are sensitive to vibration, (2) possess very small (single-digit) receptive fields, and (3) do not connect to the opposite hand representation through the corpus callosum. These criteria all point to Brodmann's area 3b. In the hand representation of this area, most neurons have single digit receptive fields (Merzenich et al., 1978; Iwamura et al., 1993), and there are virtually no callosal projections between hemispheres (Killackey et al., 1983). Furthermore, neurons in area 3b explicitly encode information about low-frequency vibration, firing in phase with each stimulus cycle of mechanical vibrations (Mountcastle et al., 1969, 1990; Hernández et al., 2000). Even more convincing are recent investigations showing that electrical stimulation of neurons in area 3b at a particular frequency produces sensations that monkeys treat as identical to a mechanical vibration of that frequency (Romo et al., 1998, 2000). Thus, we speculate that training with one fingertip to discriminate between vibration frequencies induces modifications among populations of neurons located in the topographically matching columns of area 3b. One outcome of these modifications may be to sharpen the tuning of neuronal responses to the indentation cycles of the vibration (Recanzone et al., 1992; Wang et al., 1995), thereby enhancing the signal-to-noise ratio of the sensory response and so improving the fidelity of the stimulus representation.

Punctate pressure and roughness discrimination

The learning of punctate pressure and roughness discrimination transferred to the finger neighboring the trained one and to the finger symmetrically opposite the trained one. Applying the logic used above, we seek a cortical field in which neurons (1) are sensitive to punctate pressure and static surface texture, (2) possess multidigit receptive fields, and (3) transmit information to the opposite hand representation through the corpus callosum. These criteria rule out area 3b.

The other topographically organized regions of somatosensory cortex that process cutaneous input are areas 1, 2, 5, and 43 (usually referred to as SII, the second somatosensory cortex)

(Kaas and Pons, 1988). In each of these areas, the majority of neurons have receptive fields that include more than one finger (Robinson and Burton, 1980; Iwamura et al., 1993, 1994), and there are callosal projections connecting homotopic sites in each hemisphere (Killackey et al., 1983; Manzoni et al., 1984; Krubitzer and Kaas, 1990; Iwamura et al., 1994; Iwamura, 2000). The potential contribution of these areas is considered below. However, the conclusions we reach are tempered by the difficulty in applying some of the previous evidence about roughness discrimination to the present work. In most earlier studies, subjects were allowed to rub their fingers along the surface or else the surface was moved under the subject's fingertip. Thus, these studies may have involved motor as well as sensory learning, and the sensory information could be encoded by a combination of rapidly adapting and slowly adapting neurons. In contrast, we asked subjects to sample the sandpaper by pressing their fingertip against the surface; our task would not be expected to involve motor learning, and the sensory information would be encoded primarily by slowly adapting receptors.

Area 1

Evidence that area 1 contributes to roughness and texture processing comes from reports that lesions confined to this region produce deficits in learning or retention of roughness discriminations in monkeys (Randolph and Semmes, 1974; Carlson, 1981). However, physiological recordings of neuronal activity in area 1 have yielded very few neurons that give maintained responses to constant pressure (Sinclair and Burton, 1991; Tremblay et al., 1996); the large majority have rapidly adapting responses that do not carry sufficient information about spatial structure to contribute to representations of texture (Phillips et al., 1988; Johnson and Hsiao, 1992). Moreover, because there are only sparse callosal projections connecting the area 1 hand regions (Killackey et al., 1983), this area may not permit the contralateral transfer of pressure and roughness learning that we observed.

Area 2

Despite their multidigit receptive fields and relatively dense callosal connections, it is unlikely that neurons in area 2 contribute to learning of pressure and roughness discrimination because the majority have receptive fields activated by deep tissues and joints (Hyvärinen and Poranen, 1978; Iwamura et al., 1993). Those neurons with cutaneous inputs have rapidly adapting properties (Tremblay et al., 1996). It is noteworthy that, in monkeys, learning of a roughness discrimination was completely unaffected by lesions to area 2 (Randolph and Semmes, 1974; Carlson, 1981).

Area 5

Evidence that area 5 may contribute to discriminations of texture or pressure comes from a report that lesions confined to this area produce a moderate increase in thresholds for roughness discrimination (Murray and Mishkin, 1984). However, a positron emission tomography (PET) imaging study in humans has shown that this area may be more involved in tactile processing of shape rather than roughness (Roland et al., 1998).

Area 43 (SII)

Loss of roughness discrimination ability has been reported after lesions to SII in humans (Caselli, 1991) and monkeys (Murray and Mishkin, 1984). This is consistent with the fact that roughness discrimination is also disrupted by lesions to areas 3b and 1

(Randolph and Semmes, 1974; Carlson, 1981), the main sources of cutaneous sensory input to SII (Pons et al., 1992). In monkeys, SII neurons appear to encode surface texture (Sinclair and Burton, 1993; Tremblay et al., 1996; Jiang et al., 1997). In fact, PET imaging studies with humans show that SII is significantly more active during discrimination of roughness than of other tactile features (Ledberg et al., 1995; Roland et al., 1998).

In summary, we believe that the weight of evidence discounts a role for areas 1, 2, and 5. The data point most strongly to a role for SII as an essential neural substrate for learning about roughness and pressure information.

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