

Task- and Subject-Related Differences in Sensorimotor Behavior during Active Touch

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Abstract Rats explore objects by rhythmically whisking them with their mystacial vibrissae. On two types of tactile discrimination tasks, macrogeometric and microgeometric, better performers palpated the discriminanda for longer periods of time and used movement patterns that appeared to optimize whisking frequency bandwidth and the extent to which the vibrissae would be bent by object contact. On a task involving finely textured surfaces, good and poor performers differed in the temporal components of their whisking patterns, whereas the spatial domain was more important for animals palpating surfaces with widely separated features. These findings are consistent with increasing neurophysiological evidence that the central representation of the tactile periphery, in rodents and other mammals, is both integrative and dynamic.

Key words vibrissae, tactile, texture, whisking, discriminative touch, motor control, learning

Tactile recognition of an object's texture or shape is enhanced by movement of the skin surface over it. Perhaps because they are subtle, systematic variations in active touch during different sensory tasks and/or by different observers have not been widely reported (Lederman, 1974; Lamb, 1983; Vega-Bermudez et al., 1991). Determination of information-seeking strategies employed by skilled observers, however, may reveal how individuals construct internal representations of palpated objects (Lederman and Klatzky, 1987), and may provide further insights into brain mechanisms underlying perception and other cognitive abilities.

In the present study, we used video-based motion analyses to examine in detail whisker movements of animals trained to perform one of two different tactile discrimination tasks. The mystacial vibrissae, or whiskers, consist of an array of ~30 specialized hairs on each side of the face that together are repetitively swept back and forth at 6–9 Hz (Welker, 1964; Carvell and Simons, 1990). Forward motion (protraction) is produced by active contraction of "sling" muscles surrounding each hair follicle, whereas retraction results largely from the passive recoil of viscoelastic facial tissues (Dörfl, 1982; Carvell et al., 1991). Previously (Carvell and Simons, 1990), we reported that rats using their whiskers are able to distinguish differences in surface

texture at a level comparable to that of primates using their fingertips; furthermore, across species the movement velocities employed are similar (Morley et al., 1983; Essick and Whitsel, 1985). Our earlier results also suggested that individual animals may differ with respect to the movement strategies they employ. Here we report that whisking patterns are correlated with the performance abilities of individual animals and with the nature of the surfaces being palpated.

MATERIALS AND METHODS

Surgery and Blindfolding

Several weeks prior to the initiation of behavioral testing, adult female rats were custom-fitted with removable blindfolds. Under halothane or pentobarbital sodium anesthesia, the dorsal surface of the skull was exposed by a midline scalp incision, and a dental acrylic cap was anchored to it by means of small stainless steel screws. A threaded bolt was embedded in the acrylic, and the skin was apposed to the acrylic with nonabsorbable prolene sutures. The bolt was used subsequently to secure a blindfold constructed from thermal-pliable splinting material (Orthoplast). After the wound healed, the animals were gradually acclimated to being handled by the experimenters and to wearing the

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blindfolds. These were worn only during the testing sessions, which lasted 60–90 min.

Behavioral Testing

The blindfolded rats were trained to perform a forced two-choice discrimination task (Carvell and Simons, 1990). Each animal stood on an elevated platform and stretched across a gap to palpate with its vibrissae textured surfaces that were interchangeably attached to the front of two other elevated stands; to obtain a food reward, the animal had to jump onto the appropriate stand. As described previously, the separation of the platforms was such that animals were unable to palpate both surfaces at the same time with whiskers on one side of the face. Although animals could simultaneously touch the right surface with the right whiskers and the left one with the left whiskers, they rarely did so. The rats typically palpated one surface at a time, using whiskers on both sides of the face. Variably, animals would separately explore one or both surfaces on any given trial. As reported previously, the probability of a correct choice was slightly greater when a rat sequentially sampled both surfaces.

The food reward consisted of Purina Rat Chow powder mixed with water and peanut butter. Several hours after the daily training session, animals were allowed access to food for 30–45 min. Water, but not food, was available *ad libitum* in the animals' home cages. Animals displayed weight gain and good health throughout the course of the study.

Discriminanda were constructed from Delrin plastic cylinders that were mounted horizontally on the front of the choice platforms. The cylinders were turned on a lathe to produce grooves that were perpendicular to the long axis of the cylinder and to the plane of whisker movement. Initially, all cylinders were rounded and smoothed with a diamond lathing tool; this produced a surface having fine continuous grooves that were $\sim 15 \mu\text{m}$ wide and $5 \mu\text{m}$ deep. One group of animals ($n = 7$), denoted "rough-smooth" or RS, learned to distinguish between such a cylinder and one onto which were cut a second set of grooves of equal depths, widths, and spacings of 500, 250, 200, 150, 100, 75, or $50 \mu\text{m}$. Because of the fine spatial frequencies, we describe these RS tasks as "microgeometric." Mastery of a surface was defined as $>85\%$ correct choices for 3 consecutive days with 1 of the days at 100% (10–14 trials per day); upon reaching criterion, animals progressed to successively finer surfaces. After a period of initial training using coarser discriminanda, animals required an average of 4.6 days to progress from one pairing to the next. One animal failed to learn the 100- μm task; all others completed the entire battery. A second group of RS animals ($n = 5$) was trained in a later phase of the study, in which we examined the animals' ability to perform the task following removal of different combinations of whiskers (see below).

Another group of animals ($n = 6$), denoted "rough-rough" or RR, was similarly trained to distinguish

a discriminandum having 1-mm-deep grooves of 1-mm widths and spacings from a cylinder having 1-mm-deep grooves of equal widths and spacings of 3.0, 2.0, 1.75, 1.50, 1.25, 1.125, or 1.06 mm. We describe these discriminanda, which had widely spaced features, as "macrogeometric." Because this task was more difficult, the criterion for successful performance was set at $>75\%$ correct for 3 consecutive days. On average, animals required 7.8 days to progress from one pairing to the next. Two animals failed to master the 1.125-mm discrimination during 25 days of testing on that problem; by that time, the animals displayed intractable right-left biases or no longer attended to the task. Although these animals were removed from testing, their whisking patterns are included in the biometric analyses.

Data Collection and Analysis

A SuperVHS camcorder (Panasonic AG-450), equipped with a macro lens and an electronic shutter (0.001 sec), was positioned above one of the two choice platforms. Data were recorded, digitized, and analyzed at 60 fields/sec (Peak Performance Technologies). Data were obtained from the onset of surface contact to the time when the animal either moved toward the platform (to jump onto it) or retreated to palpate the other discriminandum. Measurements were made at the bases of four vibrissae (two right, two left), and the shape of the whisker was reconstructed by measurements made at five points in 0.5-cm increments along its shaft; this was accomplished by means of specially designed cursor-positioning software that established a given radius of movement from a previously defined location. The position of each marked point was defined as the angle between the hair shaft and the side of the face. Figure 1 schematically illustrates how the measurements were made.

Results are based on analyses of four whiskers in 6006 video fields from 180 trials. Because each of the more than 25,000 data points had to be determined by visual inspection, we tried to reduce the potential for variability in the data set by selecting for detailed analysis only trials in which the animal ultimately made a correct choice. Data were collated and analyzed with software from Peak Performance, Lotus, and SPSS, and with our own custom programs. Whisker movement patterns were reconstructed from the measurements made on successive video fields. Discrete Fourier transforms (2- to 30-Hz bandwidth) were performed for each whisker's movement during a trial. Each transform provided a measure of the proportional contribution of a given frequency to the overall pattern. For each trial and whisker, we subdivided the power spectrum into four domains (2–6, 7–12, 13–17, and 18–27 Hz), determined the relative proportion of power for each of the domains, and then averaged across all trials for individual animals. Whisker deformation was calculated as the difference in the

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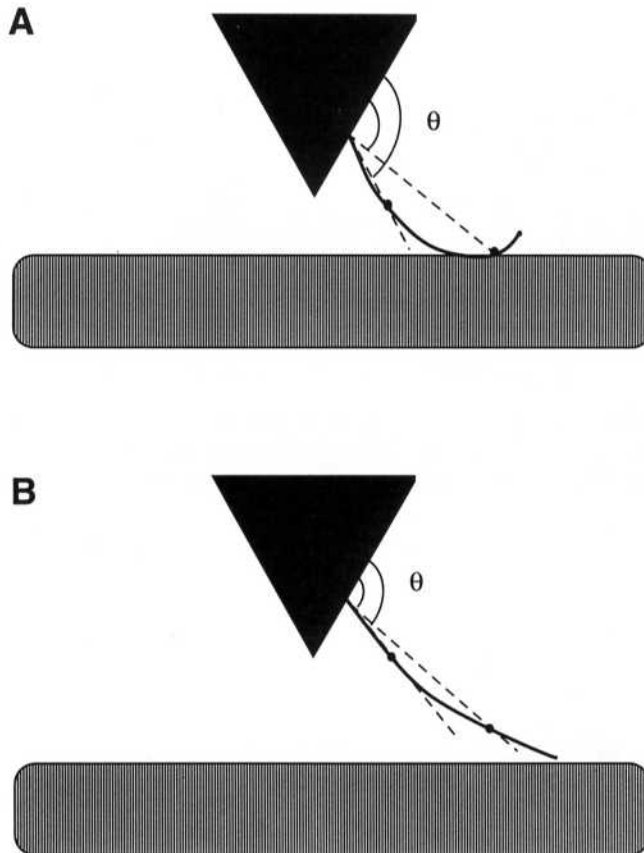


FIGURE 1. Schematic illustration of procedure for measuring whisker position and bending. The darkly shaded triangle represents the rat's head, and the lighter-shaded rectangle represents the discriminandum. A single whisker is shown contacting it in A, where the hair shaft is noticeably bent. Two dots represent measured points 1.0 and 2.5 cm along the hair. A straight line from the base of the hair to the point is used to calculate an angle (θ). Whisker bending is quantified as the difference between the arcs subtended for the 1.0- and 2.5-cm points. In B, which in this illustration would correspond to the next field (16.67 msec later), the whisker is more retracted and less deformed. Movement amplitude and velocity can be derived by finding the difference between corresponding data points (1.0 or 2.5 cm) in A and B. Drawings are not to scale.

angular positions of the whisker measured at 1.0 and 2.5 cm from the base of the hair. Larger deformations produced greater angular differences (see Fig. 1). Bending data were analyzed only for those fields in which the whisker contacted the discriminandum.

The average whisker position, or set point, was calculated from individual video fields as the average angular position of each whisker. A single whisking sweep was defined as two or more consecutive fields during which the whisker moved $\geq 2^\circ$ in the same direction. These latter analyses allowed us to calculate the amplitude and velocity of individual protraction or retraction sweeps. Amplitude

was expressed in degrees of whisker movement, and sweep velocity was calculated as follows: angular excursion/(no. of fields \times 16.67 msec). We similarly determined the time spent palpating the surface on each trial and the number of sweeps/sec/trial (a measure somewhat different from the Fourier power spectrum).

RESULTS

Task-Related Differences

Quantitative comparisons of whisking biometrics revealed four task-related differences, summarized in Figure 2. As a group, animals trained on the RS task displayed (1) smaller-amplitude and (2) lower-velocity whisking sweeps, (3) less whisker bending, and (4) a more protracted average whisker position. On each of these measures, differences between the two groups of animals were highly significant (*t* tests, all *p*'s < 0.001). On the other hand, RS and RR animals did not differ (*p*'s > 0.05 , data not shown) in terms of the average number of sweeps/trial (13.0 vs. 13.1) or palpation times (552 vs. 563 msec), and hence the average number of sweeps/sec (23.5 vs. 23.3). Also, as groups, RS and RR animals displayed similar proportions of 7- to 12-Hz frequency components in their whisking spectra (0.392 vs. 0.423, *p* > 0.05).

Performance-Related Differences

Examination of the data demonstrated differences not only across tasks but also among individual subjects, and the latter in many cases were correlated with overall performance. An example from a single whisking sequence during an individual trial is illustrated in Figure 3. Traces show whisker movements of the animal that performed the RS task with the fewest errors (KO) and the animal that made the most (RB). Compared to KO, RB spent less time palpating the surface and made more whisking sweeps/sec. Fourier power spectra are shown in the inset. The frequency spectrum of KO's whisking is characterized by a prominent modal peak at 6–8 Hz, whereas RB's contains a broad peak centered at 17–18 Hz. Data from all of the animals are presented in Figure 4A. Scatterplots show that for both tasks, good performers used whisking patterns that were dominated by frequency components in the range of 7–12 Hz. Animals that made more errors had broader power spectra (see also below).

The remaining panels in Figure 4 show data from other measures of whisking, which were similarly related to performance on the RS and RR tasks. Better performers displayed less bending of the whisker hairs (Fig. 4B), as well as a less protracted average whisker position, or set point, about which the hairs moved (Fig. 4C). Good performers generally spent longer periods of time palpating the discriminanda as well (Fig. 4D). This relationship was robust for the RS task, and with the exception of one animal, a significant

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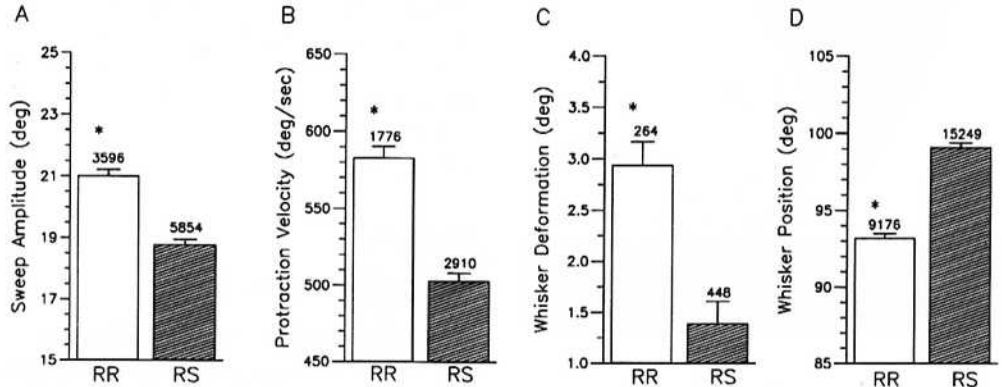


FIGURE 2. Task-related parameters of whisking. Each panel shows means and SEMs obtained from six RR and seven RS animals. Numbers above each bar indicate the number of observations upon which the measure is based. Asterisks denote statistically significant differences between data for RR and RR animals (t tests, p 's < 0.001). Note that in D, a larger value for whisker position reflects a more protracted set point.

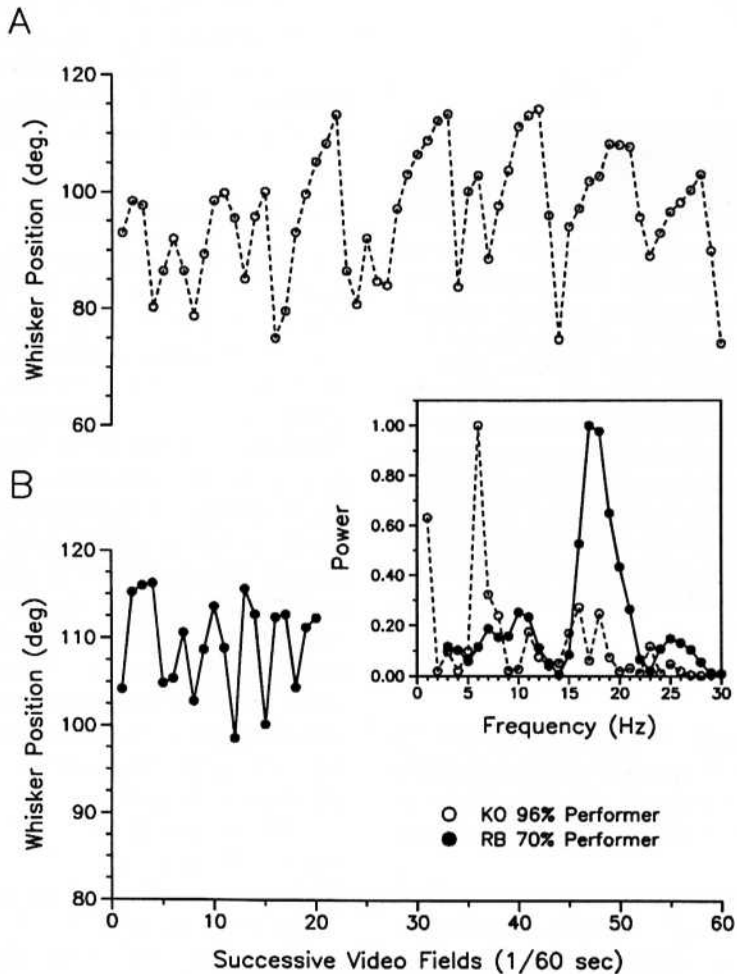


FIGURE 3. Whisking patterns of the best performer (A and open circles) and worst performer (B and filled circles) on the RS task. Graphs plot one whisker's movements during a single trial. Each data point shows whisker position measured in a given video field. Forward motion (protraction) is indicated by larger numbers on the ordinate. Note differences in frequency and time on task. Inset shows Fourier power spectra for the whisking in A and B.

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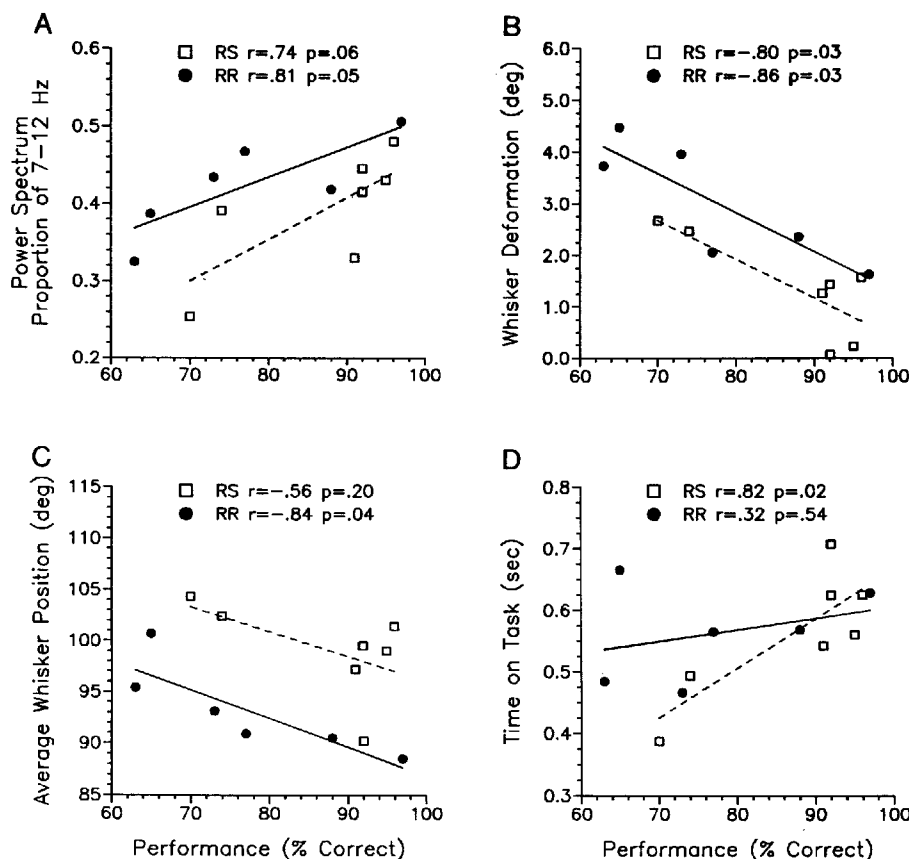


FIGURE 4. Whisking parameters found to be correlated with performance in both RS and RR animals. Each panel shows scatterplots and Pearson product-moment correlations between overall performance and one biometric measure of whisking ($n = 7$ RS, $n = 6$ RR). Each point plots data from a single animal, averaged over four whiskers and all trials. Regression lines are given as dashed lines for RS data and as solid lines for RR data.

correlation was observed for the RR task as well (for the remaining five RR animals, $r = 0.89$, $p < 0.05$).

The relationship between protraction velocity and performance on either task was not robust (Fig. 5). Neither correlation coefficient reached statistical significance, although removal from the analyses of the outlying point in the RR group (the 63% performer) yielded a stronger correlation that nevertheless was still not significant ($r = 0.87$, $p = 0.06$). Interestingly, the weak relationship was opposite for the two tasks. Higher velocities were somewhat more likely to be associated with good performance on the RR task, perhaps reflecting the larger-amplitude whisks employed by the better performers. On the RS task, better performance was more likely to be accompanied by lower protraction velocities. As will be described next, performance on this task appeared to be associated more generally with the overall rhythm of whisking.

Figure 6 shows data for those aspects of whisking that were related to *both* individual performance and task. Among animals trained on the RS task, better performers generated fewer whisking sweeps/sec (Fig. 6A). Correspondingly, RS animals displayed a robust negative correlation

between overall performance and the presence of high-frequency (18- to 27-Hz; see Fig. 6B), but not low-frequency (2- to 6-Hz; $r = 0.31$, $p = 0.50$) components in the animals' whisking power spectra. Neither of these parameters was strongly correlated with performance on the RR task. On the other hand, overall success on the macrogeometric but not the microgeometric surfaces was highly correlated with movement amplitude (Fig. 6C). Thus, temporal characteristics of whisking may have been critical factors in the performance of the RS task, whereas spatial factors may have been more important for the RR one.

Effects of Reducing the Size of the Whisker Field on Discrimination Ability

Since performance on the micro- and macrogeometric tasks appeared to be affected differently by temporal and spatial characteristics of whisking, we examined the ability of five RS and four RR animals to perform their respective discrimination tasks after their vibrissal fields were spatially altered by reducing the number of whisker hairs that were long enough to contact the discriminanda. Rats had their whiskers

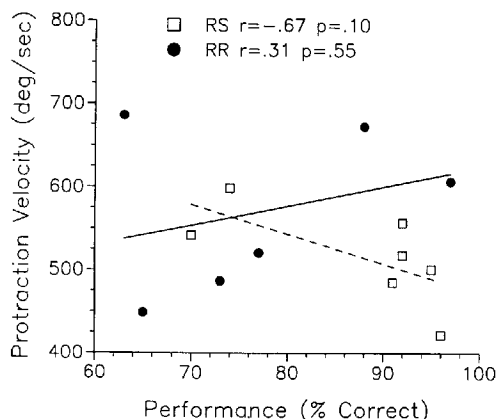


FIGURE 5. Scatterplot showing relationship between protraction velocity and performance in RS and RR animals (see text). Conventions as in Figure 4.

trimmed weekly to within 2–3 mm of the skin surface; even though the whiskers regrew between trimmings, they remained too short to reach the choice platforms. Each animal had previously mastered the 50- μ m (RS) or 1.06-mm (RR) discrimination. A separate group of RS animals was trained for this aspect of the study. Animals were tested as long as they demonstrated progress.

Figure 7 shows the effects of progressively reducing the number of vibrissae on each side of the face to a single row containing five whiskers, to two adjacent whiskers in that row, and to a single whisker. Following each reduction in the size of the whisker array, animals were retrained to criterion performance levels. Even when only one whisker was present on each side, all RS subjects were eventually able to distinguish the 50- μ m surface from the smooth one. By contrast, only one animal successfully performed the RR task with a single whisker; the remaining RR animals required two or more. We have not yet examined biometric data from the animals as they performed the task with reduced whisker fields.

DISCUSSION

Four major findings emerge from this study. First, some features of whisking behavior appear to be associated with good discrimination ability, regardless of the nature of the surfaces being palpated. Second, individual animals differ with respect to both their overall sensory discrimination performance and their motor patterns. Third, whisking behavior differs in detail between animals trained to discriminate between finely textured surfaces and those trained to detect differences between surfaces having widely spaced features. Fourth, and related to the third point, whisking variables of importance for the successful performance of one type of task are not necessarily associated with good performance on a different one. These conclusions pertain to an animal's *overall* performance. We have not yet examined in detail whether a correct or incorrect choice on any

given trial is related to the whisking pattern used during that trial. In this regard, the biometric measures obtained here may be sufficient to reveal general strategies that animals adopt; however, performance on any given trial is probably more closely related to the detailed microgeometry of whisker–surface interactions, thus requiring higher spatial and temporal resolution.

The present findings and those of our previous study (Carvell and Simons, 1990) suggest that the effective use of vibrissae during active touch is related to how the animal

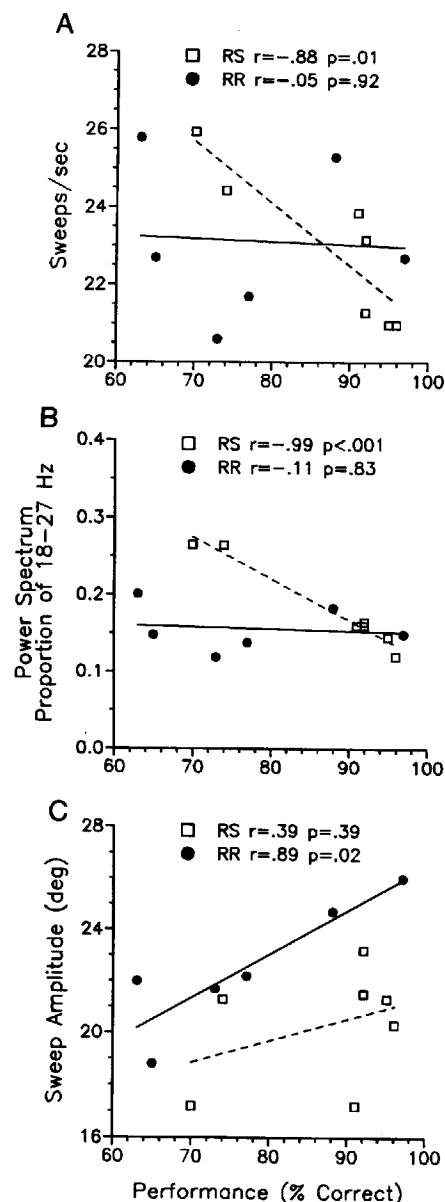


FIGURE 6. Movement parameters related to performance on either the RS or RR tasks. Performance on the RS task is related to number of sweeps/sec (A) and the proportion of high frequencies in the whisking power spectrum (B), whereas performance on the RR task is correlated with sweep amplitude (C). See also text. Conventions as in previous figures.

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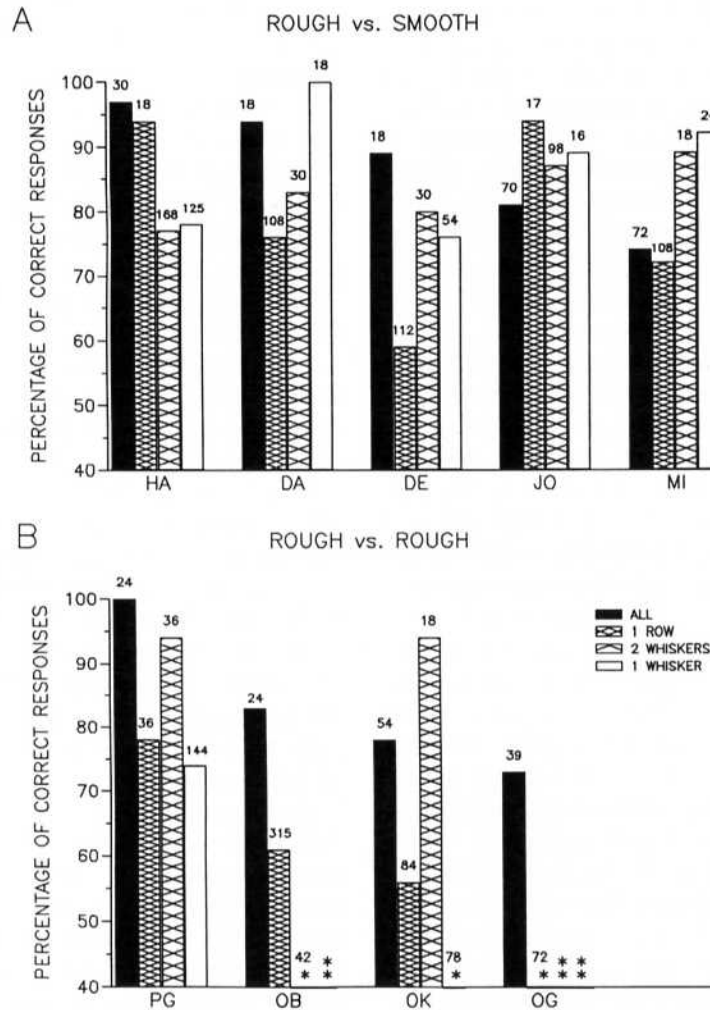


FIGURE 7. Effects of progressive whisker field reduction on discrimination abilities of individual animals. Animals (denoted by their initials) are ordered on the abscissa according to overall proficiency when all whiskers were intact. The number above each bar represents the number of days required to reach criterion performance. Asterisks denote the inability of the animal to master the task within the number of days indicated above the bar. Double asterisks indicate that the animal was not tested under this condition because it failed to master the task when more whiskers were present.

moves its whiskers. In the whisker system, as in others, tactile sensitivity probably is enhanced by relative movement of an object across the receptor periphery. Whisking is a highly integrated motor behavior that also involves carefully timed movements of the head and body and, during exploration, of respiratory muscles as well (Welker, 1964). Our observations that good performance is associated with a specific range of whisking frequencies and with the maintenance of an apparently optimal amount of whisker bending (and thus, perhaps, force) indicate the importance of accuracy in and coordination of the motor pattern. Good performers generally spend more time on task, and, as we reported previously, a correct choice is more likely to occur when the animal palpates both surfaces during a trial. The perceived intensity of vibrotactile stimuli in human observers increases with stimulus duration to a maximum of ~1 sec (Berglund

et al., 1967), and humans distinguishing between textured surfaces perform better when allowed to resample the discriminanda during a trial (Sinclair and Burton, 1991a). Together, the findings suggest that in the present study, skilled animals employed movement strategies that optimized both the acquisition of information inherent to the external object and the time-dependent synthesis of its internal representation.

The RS task could be regarded as one that requires simple detection of the presence or absence of surface features, rather than as one requiring discrimination of detailed surface topographies. On the other hand, bending of the whiskers by contact with either surface undoubtedly activates peripheral mechanoreceptors, and their surface-related signals must somehow form the basis for the perceptual differences. Since we have found that the amount of whisker bending is comparable for palpation of the smooth and the

rough surfaces, and since there must be some friction between the whisker hair and even the smooth surface, it is highly likely that the animals are detecting differences in the amplitude and/or frequency of microvibrations of the hair shaft. If mystacial pad muscle contraction helps to stiffen tissue surrounding the hair follicles, then the greater muscle activity associated with more protracted set points (Carvell et al., 1991) might increase the sensitivity of the mechanoreceptors responsive to whisker vibrations. This could explain the finding that RS animals employed more protracted whisker set points than RR animals.

For animals trained on the RS task, good performance was associated with fewer whisking sweeps/sec and with a relative absence of high-frequency components in the whisking pattern. These findings are consistent with the importance of *temporal* neural codes in the sensory discrimination of microgeometric surfaces. Detection of fine textures is thought to depend on activity in peripheral mechanoreceptors that can be entrained by high-frequency vibrations (Katz, 1989; Srinivasan et al., 1990). Even at the lowest average protraction velocity (422°/sec), a point 15 mm along a hair shaft passing over the 100- μ m grating would contact a ridge >1000 times/sec. Although this frequency is within the response range of some whisker follicle receptors (Gottschaldt and Vahle-Hinz, 1981), it is too high for the entrainment of spike discharges of individual neurons in central somatosensory pathways (Mountcastle et al., 1969; Hellweg et al., 1977; Simons, 1978). As proposed for texture recognition by finger palpation (Darian-Smith et al., 1982; Sinclair and Burton, 1991b), the central representation for the microgeometric surfaces used here may involve a signal based on mean neuronal firing rate. Whatever the code, it is likely to be embedded within a pulsatile neuronal discharge that accompanies individual whisking sweeps. Studies in progress indicate that somatosensory cortical neurons discharge in synchrony with whisking as the vibrissae of trained animals contact a surface at intervals of \sim 125 msec. Stimulus-evoked excitatory responses in central vibrissa neurons are typically followed by a time-dependent inhibition with a duration of 100–150 msec (Carvell and Simons, 1988; Salt and Eaton, 1990; Kyriazi et al., 1994). Thus, whisking patterns having too many high-frequency components would include inappropriately timed whisker perturbations whose information content might be altered by the inhibition established during a prior whisker deflection.

Sweep amplitude and average whisker position were correlated with good performance on the RR task. Also, three of the four animals tested required the presence of two or more whiskers to perform the task successfully. In this task, surface features are spaced at least 1 mm apart. Together, the findings suggest the importance of spatial aspects of the sensorimotor behavior. Perhaps animals that can better control the range of their whisker movements are better able to scan the relevant features of the macrogeometric

surface during each individual sweep. This is consistent with the present findings that, compared to RS animals, RR animals employed larger-amplitude sweeps; this in turn may account for the greater amount of whisker bending that these rats displayed. Greater surface-induced bending sustained over a larger surface area may lead to more effective use of signals arising from slowly adapting primary afferent fibers, which in primates are thought to be critically important for tactile form perception (Darian-Smith et al., 1980; Connor and Johnson, 1992; see also Goodwin and Morley, 1987).

At a point along the hair shaft 15 mm from the skin surface, 3.81° of angular excursion corresponds to 1 mm of length along the discriminandum. In the case of the 1.125-mm surface, the distance between successive ridges is well within the average single sweep range (\sim 20°) of even the poorest performers. Moreover, the bending of the whisker hair is large enough, particularly for the longer whiskers, for it to contact 4–5 mm of surface length. However, for the RR task, the area that a *single* whisker contacts appears to be not as important as the surface area palpated by two or more adjacent vibrissae. In the absence of surface contact, the distal segments of the larger, caudal whiskers are separated by at least 5–10 mm, but this separation is greatly reduced when the whiskers touch the discriminandum. For technical reasons relating to spatial resolution and depth of field in viewing whiskers overlaying the curved discriminandum, we have not been able to make the appropriate measurements. Nevertheless, our observations suggest that the likelihood of nearby vibrissae contacting adjacent ridges simultaneously or in close temporal succession should be increased if the animal employs larger-amplitude movements, as observed in this study for RR animals. It has been proposed that in the case of primate fingertips, perception of rough surfaces having features spaced several millimeters apart is mediated by central neuron populations that are sensitive to differences in the firing patterns of mechanoreceptive afferents innervating nearby regions of skin (Connor and Johnson, 1992). In the whisker system, central neurons, unlike primary afferent fibers, display complex excitatory and inhibitory interactions among inputs from nearby whiskers (Simons, 1985; Armstrong-James and Fox, 1987).

In the absence of primary somatosensory cortex, rats are severely impaired in their ability to make vibrissal-based texture discriminations similar to those used here (Guic-Robles et al., 1992). In rats and other rodents, this cortex is characterized by the presence in layer IV of morphologically identifiable neuronal networks, called "barrels," that are related in a one-to-one manner to individual whiskers on the contralateral face (Woolsey and Van der Loos, 1970; Welker, 1971). Barrel circuitry transforms afferent signals from the thalamus (Simons and Carvell, 1989; Kyriazi et al., 1994), and outputs are directed to neurons in other layers of the same and nearby cortical columns (Bernardo

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et al., 1990; Armstrong-James et al., 1992). Thus, whereas most barrel neurons respond vigorously to deflections of only one or a few whiskers, neurons in supra- and infragranular layers have receptive fields that typically encompass many vibrissae (Simons, 1978; Armstrong-James and Fox, 1987). In light of the RR animals' inability to perform their task with a single whisker, these neurophysiological findings suggest that intercolumnar connections within the barrel cortex are critically important for detecting differences between macrogeometric surfaces. Though less completely studied, neurons in the second somatosensory cortex have multi-whisker receptive fields (Welker and Sinha, 1972; Carvell and Simons, 1986), and this area could be important as well for discriminating macrogeometric surfaces.

ACKNOWLEDGMENTS

We thank Melissa Bodner for assistance in training the animals; David Grundy for computer programming; and Judy Kodger for animal training, video data analysis, and data collation. This research was supported by NSF Grant Nos. BNS8909620 and IBN9209490.

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