Receptive Fields and Response Properties of Neurons in the Star-Nosed Mole’s Somatosensory Fovea

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Received 12 July 2001; accepted in final form 10 January 2002

Sachdev, Robert N. S. and Kenneth C. Catania. Receptive fields and response properties of neurons in the star-nosed mole’s somatosensory fovea. J Neurophysiol 87: 2602–2611, 2002; 10.1152/jn00576.2001. Star-nosed moles have an extraordinary mechanosensory system consisting of 22 densely innervated nasal appendages covered with thousands of sensitive touch domes. A single appendage acts as the fovea and the star is constantly shifted to touch this foveal appendage to objects of interest. Here we investigated the receptive fields on the star and the response properties of 144 neurons in the mole’s primary somatosensory cortex (S1). Excitatory receptive fields were defined by recording multiunit activity from the S1 representations of the nasal appendages that form the star, while stimulating the touch domes on the skin surface with a small probe. Receptive fields were among the smallest reported for mammalian glabrous skin, averaging <1 mm². The smallest receptive fields were found for the fovea representation, corresponding to its greater cortical magnification. Single units were then isolated, primarily from the representation of the somatosensory fovea, and the skin surface was stimulated with a small probe attached to a piezoelectric wafer controlled by a computer interface. The response properties of neurons and the locations of inhibitory surrounds were evaluated with two complementary approaches. In the first set of experiments, single microelectrodes were used to isolate unit activity in S1, and data were collected for stimulation to different areas of the sensory star. In the second set of experiments, a multi-electrode array (4 electrodes spaced at 200 μm in a linear sequence) was used to simultaneously record from isolated units in different cortical areas representing different parts of the sensory periphery. These experiments revealed a short-latency excitatory discharge to stimulation of the fovea followed by a long-lasting suppression of spontaneous activity. Sixty-one percent of neurons responded with an excitatory off response at the end of the stimulus; the remaining 39% of cells did not respond or were inhibited at stimulus offset. Stimulation of areas surrounding the central receptive field often revealed inhibitory surrounds. Forty percent of the neurons that responded to mechanosensory stimulation of the receptive field center were inhibited by stimulation of surrounding areas of skin on the same appendage. In contrast to neurons in rodent barrels, few neurons within a stripe representing an appendage responded to stimulation of neighboring (nonprimary) appendages on the snout. The small receptive fields, short latencies, and inhibitory surrounds are consistent with the star’s role in rapidly determining the locations and identities of objects in a complex tactile environment.

INTRODUCTION

Star-nosed moles have an extraordinary mechanosensory organ on the front of their face consisting of 22 appendages covered with thousands of epidermal touch domes. Among the 11 appendages on each side of the face, a single ventral appendage (number 11) acts as a mechanosensory fovea and is preferentially used to explore objects of interest. Moles make almost constant head movements to touch different areas of the environment with the tactile fovea, just as more visual mammals constantly shift their gaze to position images on the area centralis (Fig. 1). Although the nasal appendages resemble fingers, they are not used to manipulate objects or capture prey (Catania and Kaas 1997). Instead, their function is purely mechanosensory and for this purpose each contains thousands of touch domes called “Eimer’s organs.” The star is approximately 15 mm across but is innervated by over 100,000 myelinated fibers and contains over 25,000 Merkel cell–neurite complexes and lamellated corpuscles, as well as hundreds of thousands of free nerve endings (Catania 1996; Catania and Kaas 1997).

As would be expected, the star has a large and complex representation in cortex (Catania and Kaas 1995). Both primary (S1) and secondary (S2) somatosensory cortex have distinctive cytoarchitectures and contain 11 bands of tissue representing the contralateral star. Each band in both S1 and S2 represents a single appendage and is visible in histological preparations, such as cytochrome oxidase, much like the S1 barrel system of rodents (Woolsey and Van der Loos 1970; Woolsey et al. 1975).

At present little is known about the response properties and receptive fields of individual neurons in the mole’s cortex or how the star functions to discriminate objects through touch. The mole’s star shares some features in common with disparate sensory systems, such as the rodent barrel system, mammalian fingers, or the visual system of other mammals. We wondered how information from the star was represented in comparison with other mammalian sensory systems.

In primates, for example, information from the fingers is processed in multiple large cortical areas (Kaas et al. 1979, 1983, 1987) and functional cell classes are segregated into separate modules (Sur et al. 1981, 1984). In contrast, rodent whiskers are primarily represented in a single large representation (Woolsey and Van der Loos 1970) where neurons in a single barrel are maximally excited by stimulation to a single corresponding whisker but may also be excited or inhibited by
stimulation of surrounding whiskers (Armstrong-James and Fox 1987; Nicolelis et al. 1995; Sachdev et al. 2000; Simons 1985). How is information from the star, which shares some features in common with these systems, processed in cortex? Here we begin to explore this question by investigating the responses of cortical neurons in S1. Our goal was to determine response properties that could be correlated with mechanosensory functions and to identify aspects of sensory processing that might represent general mechanisms across sensory systems.

**METHODS**

In this study recordings were made from the primary somatosensory cortex of eight adult star-nosed moles (Condylura cristata) weighing 45–60 g. Moles were collected in Potter County, PA under scientific collecting permit COL 00087. Animals were anesthetized with urethane (1.0 g/kg; ip; 15% wt/vol) supplemented with ketamine (0.1 g/kg) as necessary. Body temperature was maintained with a heating pad. The mole was placed in a head holder; a craniotomy was made to expose cortex and the brain was protected with silicone. A photograph of the cortical surface was used to mark electrode penetrations relative to blood vessels. Single tungsten microelectrodes or arrays of four electrodes (FHC, 1–2 MΩ, at 1.000 Hz) were used to record multi- and single-unit activity with penetrations perpendicular to the cortical surface. Electrode arrays were in a single row with a 200-μm inter-electrode separation. Selected penetrations were marked with a 10 μA current for 10 s.

**Stimulation**

The size and location of each receptive field on the star (Fig. 2) was initially determined by recording multiple unit activity at each electrode penetration while stimulating the skin surface of the star with a small hand-held glass probe under a surgical microscope. In S1 these receptive fields consisted of a central area of Eimer’s organs that elicited strong bursts of neuronal activity in response to very light contact with the probe. Invariably there was a sharp border to this excitatory region beyond which neuronal activity in response to tactile stimulation dropped precipitously to a level undetectable by the experimenters. These borders were marked on an enlarged schematic of the nose (Fig. 2).

At a subset of electrode penetrations, single units were then isolated and waveforms were collected while providing computer controlled mechanosensory stimulation with a piezoelectrically controlled probe at different locations relative to the previously defined receptive field. The small probe attached to a piezoelectric wafer could be adjusted to have a contact area from 0.2 to 0.5 mm across. Spike 2 software and a 1401 computer interface (Cambridge Electronic Devices, London) were used to trigger voltage pulses to the stimulator which had a rapid onset and offset (0.2-ms duration at a speed of 250 mm/s) and depressed the skin surface approximately 200 μm (orthogonal to the surface). Stimuli were delivered for durations of 5 or 500 ms with 1 s between each stimulus. The position of the probe and area of skin indentation were recorded on a schematic of the nose for each stimulation condition. After 50 trials were collected for each stimulus duration, the probe was repositioned. At each recording site, 1 min of spontaneous activity was also collected. At the end of the recording session (5–10 h) moles were perfused transcardially with phosphate-buffered 0.9% saline followed by 2% paraformaldehyde. The brain was removed and the cortex was separated from white matter, flattened between glass plates, and stored overnight in 30% sucrose in phosphate buffer. Tangential 60 μm sections were cut parallel to the surface on a freezing microtome and processed for cytochrome oxidase (Wong-Riley and Carroll 1984).

**FIG. 1.** Summary of the star-nosed mole’s mechanosensory system. A: a front view of a star-nosed mole showing the large, clawed forelimbs and the tip of the nose surrounded by 22 fleshy appendages. B: the nose is approximately 15 mm in diameter and consists of 11 bilaterally symmetric nasal appendages that surround each nostril. The relatively small 11th appendage acts as the mechanosensory fovea. Bottom panel: the sensitive, domed mechanoreceptors (Eimer’s organs) that cover each appendage. C: the location and organization of the star representation in primary somatosensory cortex (S1). Each of the 11 appendages is represented in cortex by a stripe of tissue visible in histological preparations, such as cytochrome oxidase (bottom panel). Note the greatly magnified representation of the 11th, foveal appendage, visible in the cortical section. D: star-nosed mole orienting behavior. When an object of interest is contacted with the lateral appendages (1), the nose is then immediately shifted so that contact is made with the 11th, foveal appendage (2).
significantly for glabrous skin (see text). The receptive size of the receptive primary somatosensory representation (S1) of the star. Note the small absolute greater magnification of this area in the cortex (Fig. 1C). The average size of the receptive fields was 0.59 mm² for the 11th appendage (n = 25) and 0.82 mm² for appendages 1 through 10 (n = 30), a significant difference (P < 0.001 t = 19.5, df = 53).

Data acquisition

A Multi-Neuronal Acquisition Processor (Plexon, Dallas, TX, sampling rate = 40 kHz per channel) was used to collect all waveforms and timestamps. Neuroexplorer software (Plexon) was used for on-line and off-line analysis of single-unit data. All spike sorting was done in two stages using a principal component spike sorting algorithm (Plexon). A template of average waveforms on each electrode was made on-line. The first two principal components of each waveform were then projected into x-y coordinates. Clusters corresponding to a single unit were selected on each electrode and these units were monitored with on-line poststimulus time histograms (PSTHs), interval histograms, and autocorrelograms. All waveforms that went below threshold (often including more than 1 unit) were saved to disk for off-line sorting and analysis. Two additional single units could sometimes be discriminated off-line for each electrode. Further details can be found elsewhere (Nicolelis and Chapin 1994; Sachdev et al. 2000).

Single unit data analysis

The spike latency and the average evoked firing rate of each neuron were estimated using PSTHs. The responses were assessed by making confidence intervals of the PSTH and by preparing cumulative sums of spikes generated with 1-ms bins in the 50 ms before stimulus to 100-ms poststimulus, with 10-ms bins in the 200 ms before the stimulus to 800-ms poststimulus histograms. Population histograms were generated at two binwidths (1 and 10 ms) by averaging all PSTHs generated for each stimulus condition and for each response type. The Mann-Whitney U test and the Wilcoxon matched-pairs signed-rank test were used on these data sets.

All procedures conformed to National Institutes of Health standards concerning the use and welfare of experimental animals and were approved by the Vanderbilt University Animal Care Committee.

RESULTS

In the course of this investigation, information was gathered about response latencies, receptive field size, inhibitory surroundings, and general response characteristics of neurons in S1. Multiunit receptive fields were determined across the entire representation of the star in S1; however, investigation of single units focused primarily on the representation of the 11th ventral appendage of the star, the tactile fovea. This region was most easily stimulated in the periphery and, as in visual systems, had the largest representation in cortex and the smallest peripheral receptive fields, providing technical advantages for mapping and electrode placement.

The star is approximately 15 mm across when measured from the spread tips of the lateral appendages (Fig. 1B). Consistent with its small size and high innervation density, the receptive fields were extremely small, requiring a microscope for accurate measurement. Figure 2 shows a representative sample of receptive fields defined by multiunit excitation and their variation in size across the star. The skin surface of the 11th appendage had the smallest receptive fields with a mean area of 0.59 mm² (n = 25). Receptive fields on the peripheral appendages (1 through 10) were approximately 40% larger (mean 0.82 mm², n = 30) and this difference was significant (P < 0.001). The smaller receptive fields found on tactile fovea are consistent with its greater degree of cortical magnification centrally (see Fig. 1C); however, there was no direct inverse proportional relationship between these quantities as reported in some previous studies (Sur 1980; see DISCUSSION).

For single-unit recordings, the microelectrodes were lowered into layer 4 of the 10th or 11th division of the S1 star representation. Once the receptive field at each recording site had been determined, the piezoelectric stimulator was positioned at the center of the receptive field and single-unit activity was collected. Responses to areas surrounding the receptive field were collected in a subset of neurons. For 49 neurons this included areas on the same appendage and in 68 neurons adjacent appendages were stimulated.

Ninety-seven percent (140/145) of the neurons had a significant response to stimulation of the 11th (134 neurons) or 10th (6 neurons) appendage, corresponding, respectively, to electrode placement in the 11th and 10th subdivisions in S1 (for
example, see Figs. 3 and 4). The remaining neurons (5) in the study were not modulated by stimulation to any part of the star. Of the neurons with activity modulated by tactile stimulation to the star, ninety-six percent (135 of 140) were excited by stimulation to the center of the receptive field determined from multiunit activity. Interestingly, five neurons responded to stimulation of the receptive field center with suppression of discharge followed by sustained or transient excitation (Fig. 5).

Figures 3 and 4 (top) show two typical excitatory responses to the mechanosensory stimulus applied at the center of corresponding receptive fields and illustrate the topographic correspondence between the subdivisions within S1 and the receptive fields on the star. Electrode locations were determined by making microlesions in the cortical representation of the star and relating these to penetrations marked on brain photographs (see Catania and Kaas 1995 for details). In general, the locations of the electrodes in layer 4 of S1 (bottom of figures) corresponded to the topographically appropriate areas of the histologically visible representation of the star. In Fig. 3, for example, the electrode was located in the 10th subdivision, and the receptive field that elicited multiunit activity was located at the corresponding location on the 10th appendage. Similarly, electrode penetrations in the 11th subdivision of the S1 nose representation (Fig. 4) corresponded to receptive fields on the 11th appendage of the star.

When areas surrounding the excitatory receptive field were stimulated, 31% (15/49) of the neurons responded with an excitatory discharge and 41% (20/49) of the neurons responded with suppression of the spontaneous discharge. This was demonstrated by two complementary approaches. First, when recording units from a single microelectrode at a single cortical locus, the stimulator was moved to surrounding areas of the star and activity was collected. Figures 3 and 4 (bottom) illustrate this procedure, which provided information about the responses of individual neurons to different areas of peripheral stimulation. In other cases the use of a multi-electrode array in the cortex provided simultaneous information from multiple neurons in response to stimulation of a single area in the periphery (Fig. 6). When using the multi-electrode array, neurons typically responded with excitation to center receptive field stimulation, while at the same time other neurons simultaneously recorded at an electrode spaced 200 μm distant (and having a different receptive field) often responded with inhibition (Fig. 6). Inhibition was always transient; it never lasted for the entire duration of a 500-ms stimulation. The onset latency and the duration of inhibition were variable from neuron to neuron, with a mean onset latency of 24 ms (SE = 4.9 ms, median = 8 ms, mode = 8 ms) and a mean duration of 85.1 ms (SE = 13.8 ms). However, approximately half of the inhibitory responses had a latency of under 10 ms, suggesting that much of the inhibition overlapped the typical time course of excitation (see DiCarlo and Johnson 1999). In 71% (35/49) of the neurons investigated with surround stimulation, movement of 1–2 mm off of the receptive field was sufficient to convert significant excitation to inhibition or no response (Figs. 3, 4, 6, and 7). The 14 remaining neurons investigated with surround stimulation were excited by stimulation to areas surrounding the excitatory receptive field defined by multiunit activity.

![FIG. 3. Poststimulus time histogram showing excitation and inhibition for an individual neuron to a 500-ms mechanosensory stimulus. The neuron was located in a band of tissue representing the 10th appendage and responded with excitation to stimulation of the receptive field (top histogram) and inhibition to stimulation off of the primary receptive field (bottom histogram). Bin size = 10 ms. Black bar indicates stimulus time course.](image-url)
Twenty-two percent of neurons were modulated by stimulation to an appendage that did not contain the primary receptive field (for example, see Fig. 7). Of the 64 neurons tested with stimulation to neighboring, topographically inappropriate appendages, 14% responded with inhibition, 8% responded with excitation, and 78% had no response to stimulation of adjacent appendages. The mean excitatory response onset latency at the receptive field center for all of the units investigated was 11.6 ms (SE = 0.34 ms, median = 10 ms, mode = 9 ms) with a peak of activity in the average PSTH at 11 ms (Fig. 8). These latency characteristics were independent of stimulus duration; both the 5- and the 500-ms stimulus evoked responses at similar average latencies (Fig. 7). The mean duration of the excitatory response was 46.1 ms (SE = 2.0 ms). Inhibition that suppressed the firing rate below the spontaneous firing rate followed the excitatory response in 78% (69/88) of neurons. This number does not include the 24% (34) that had a sustained excitatory response to the sustained (500 ms) stimulus. The duration of the postexcitatory inhibition was 146.2 ms (SE = 7.8 ms). At the offset of the 500-ms stimulus a response was observed in 88 of 144 neurons. This “OFF” response had a latency (12.2 ms, SE = 0.7 ms) and duration (39.1 ms, SE = 3.11 ms) that was similar to the latency and duration at the stimulus onset.

These results suggest that a large proportion of neurons in the S1 star representation respond with a short (<10 ms) latency and have small, central excitatory receptive fields and larger inhibitory surrounds. Excitatory receptive fields were usually restricted to a single, continuous patch of skin on an individual appendage. The inhibitory receptive fields were larger, but also typically restricted to the same appendage. A much smaller number of neurons (4%) responded to stimulation of the central receptive field with an initial inhibitory response (Fig. 5).

**DISCUSSION**

Star-nosed moles are mechanosensory specialists with the ability to discriminate tiny objects with remarkable speed and precision (Catania and Kaas 1997). It is clear from mole behavior that at least two stimulus parameters are accurately and rapidly analyzed during each brief touch. These are as follows: 1) the precise spatial locations of objects, and 2) object- and prey-specific features used to decide what areas in sensory space should be explored in greater detail with the fovea and then, in the case of food, eaten or rejected (Fig. 1D).

The results of the present investigation provide basic information about the response properties and receptive fields of neurons involved in this process.

**Receptive field size**

One of the striking features of this sensory system is the small size of receptive fields on the glabrous skin surface of the nose (Fig. 2). Receptive fields averaged less than a square millimeter in area, considerably smaller than the smallest receptive fields reported for many other sensitive mammalian skin surfaces, including the sensitive areas of the primate hand (DiCarlo et al. 1998; Pons et al. 1987; Sur 1980; Vega-Bermudez and Johnson 1999; Xerri et al. 1998). Receptive fields on appendages 1 through 10 averaged 40% larger than those on the 11th foveal appendage, and this dif-
ference was significant ($P < 0.001$). This finding is consistent with a general trend in mammalian sensory systems that areas with the greatest cortical magnification centrally also have the smallest receptive fields peripherally. In star-nosed moles the 11th appendage has a cortical representation approximately four times larger than many of the other appendages, despite its relatively small size (Catania 1995; Catania and Kaas 1997). Given the proportional relationship reported between receptive field size and inverse cortical magnification (for example, Sur 1980), one might predict an even greater disparity of receptive field sizes between the tactile fovea and more peripheral areas. However, cortical magnification in star-nosed moles is not proportional to peripheral innervation density (Catania 1995, Catania and Kaas 1997) as reported for some other species (Welker and Van der Loos 1986), and thus receptive fields are not expected to be as closely tied to cortical magni-

![Image](https://example.com/image1.png)

**FIG. 5.** Example of a neuron that responded to stimulation of the receptive field center with an initially inhibitory response. A: a poststimulus time histogram illustrates the response to a 500-ms mechanosensory stimulus. Suppression of spontaneous activity occurs at stimulus onset and offset. B: the receptive field location on the 11th appendage of the star. Bin size = 10 ms. Black bar indicates stimulus time course.

![Image](https://example.com/image2.png)

**FIG. 6.** Center-surround receptive field organization in the star-nosed mole demonstrated by recording simultaneously from two electrodes. A: the receptive fields and stimulation points illustrated on a schematic of the star. B: drawing of the cortical subdivisions that represent each appendage in S1 showing the location of the electrodes and reference lesions relative to each appendage representation. The two electrodes were in the 11th foveal division and exhibited the expected somatotopy; the receptive field at electrode 1 was more ventral than that of electrode 2, as would be predicted from their respective locations in cortex. C: stimulation on the receptive field center for a neuron recorded at electrode 1 resulted in its excitation (top) but inhibited the nearby neuron recorded at electrode 2 (bottom). D: stimulation at a point off of the receptive fields of both neurons inhibited spontaneous activity at both electrodes. C and D: y axis represents counts/bin.
The functional significance of the disparity between cortical magnification and innervation density in star-nosed moles is unclear; however, it seems reasonable to presume that there is an advantage in processing speed or accuracy (or both) derived from devoting the most neuronal tissue to afferents from the important, foveal part of the sensory periphery. A similar over-representation of sensory inputs has been reported in the case of foveal ganglion cells in the visual system of primates (Azzopardi and Cowey 1993).

FIG. 7. These poststimulus time histograms show the distance effect that transformed a strong excitatory response into inhibition as the stimulus was moved from the center of the receptive field to more distal and distant areas. At the center of the receptive field (shaded area on appendage 11 right), the neuron responded with a strong sustained discharge (top histogram). When the stimulus was moved distally on appendage 11, the neuron was inhibited for a duration of approximately 40 ms. Inhibition of spontaneous activity extended to stimulation of nearby areas of appendage 10, but not to more distant parts of appendage 10 (bottom) or other appendages (not shown). In this case, the electrode was located in the 11th subdivision of S1, at the location of the left lesion illustrated in Fig. 6B.
Surround inhibition

Inhibitory responses to tactile stimulation off of the central receptive field were a prominent feature in S1. Suppression of activity could only be determined in neurons with a robust spontaneous discharge, and therefore, our estimates of the number of neurons with inhibitory surrounds were conservative (see Gardner and Costanzo 1980; Laskin and Spencer 1979; Mountcastle 1957). Nevertheless, inhibitory surrounds on the same appendage were found for 41% of neurons investigated.

The classic functional interpretation of surround inhibition is a sharpening effect that increases the contrast of discrete sensory stimuli (Békésy 1958; Gardner and Costanzo 1980; Laskin and Spencer 1979; Mountcastle 1957; Ratliff and Hartline 1959). Star-nosed moles make almost constant saccade-like head movements to accurately reposition the fovea on objects of interest (Fig. 1D and see Catania and Kaas 1997) and this is often followed by a carefully directed bite when a small invertebrate prey has been discovered. Determining the precise spatial locations of objects is certainly one of the fundamental roles of the star. As has been suggested for other systems (Békésy 1958; Crook et al. 1998; Fujita and Konishi 1991; Mountcastle 1984; Ratliff and Hartline 1959; Stanford and Hartline 1980; Suga 1995), surround inhibition may refine the activity derived from sensory inputs to facilitate stimulus localization. For star-nosed moles, a reasonable strategy for accurate foveation is to move the center of the tactile fovea to the center of the object of interest. By limiting the spread of excitation, inhibitory circuitry could restrict the locus of strongest cortical excitation to a relatively small area in S1 (Fig. 9), thus providing the central topographic substrate for the appropriate motor response.

Modular cortex and neuronal activity

The organization of somatosensory cortex in star-nosed moles is similar in some respects to the barrel cortex of rodents (Woolsey et al. 1975). In rats, for example, the representation of the large mystacial vibrissae is visibly reflected in tangential

![Diagram of surround inhibition](image-url)
sections of S1 cortex processed for cytochrome oxidase and other histochemical markers (Woolsey and Van der Loos 1970). Similarly, the representation of the star in S1 is visibly reflected in cortex by a series of stripes that are isomorphic with the distribution of mechanoreceptors in the periphery (Fig. 1). Given these similarities, we wondered how similar cortical activity patterns would be across these two systems.

Of particular interest is the degree to which information from a discrete set of peripheral mechanoreceptors is processed in a single corresponding module in cortex. Early studies of rodent barrel cortex, using barbiturate anesthetics, suggested that deflection of a single whisker in the periphery elicited neuronal activity almost exclusively in a single cortical barrel (Welker 1971, 1976). However, more recent studies indicate that deflection of a single whisker reliably activates neurons in both the topographically corresponding barrel and the neighboring barrels (Armstrong-James and Fox 1987; Ghazanfar and Nicolelis 1999; Nicolelis et al. 1995; Simons 1978, 1985).

In contrast, our results from star-nosed moles suggest (based primarily on responses in the 11th division of the cortex) that stimulation of a single star appendage results in activation of neurons restricted primarily to the corresponding subdivision in cortex. Of 64 neurons tested with stimulation to nonprimary, neighboring appendages, only five were excited, whereas nine were inhibited. Activity in the remaining 50 neurons (78%) was not modulated by stimulation of neighboring appendages. Further investigation is needed to establish the degree of divergence of sensory information in the representation of additional appendages, but our preliminary results suggest that information from each nasal appendage is processed primarily in the topographically corresponding cortical module (Fig. 1C) with relatively little activation, and some inhibition, of adjacent cortical modules.

A comparison between the mole nose system and the rodent whisker system (two disparate systems in which the sensory periphery is represented by cortical modules) is instructive. Both systems are exquisitely sensitive tactile systems (Carvell and Simons 1990; Hutson and Masterton 1986) but in the whisker system the tactile surface consists of a mobile hair, whereas the mole star is a continuous dense sheet of mechanoreceptors. In some respects the cortical responses of the mole nose and rat whiskers are remarkably similar. Short-latency excitation to the center receptive field predominates in both cortices (Armstrong-James and Fox 1987; Simons 1978). There exists a class of neurons in both cortices that have a sustained response to a sustained stimulus and a class of neurons that have off responses at the end of stimuli (Simons 1978). In both cortices excitation at the center of the receptive field is followed by suppression of discharge (Simons 1978).

The most obvious difference between these systems is in their response to receptive field surrounds. In the rat barrel cortex, topographically inappropriate whiskers typically evoke an excitatory discharge (Armstrong-James and Fox 1987; Nicolelis et al. 1995) and suppression of spontaneous activity by stimulation of single whiskers is rare (but see Sachdev et al. 2000; Swadlow 1989). Inhibition in rat barrel cortex is typically demonstrated by two whisker stimulation (Shimegi et al. 1999; Simons 1978, 1985). In the mole cortical modules, stimulation of topographically inappropriate, surrounding appendages rarely modulated neuronal activity for a given appending representation. However, in contrast to the rat barrel cortex, the spontaneous activity of 41% of the neurons was suppressed by stimulation of surrounding patches of skin on the same appendage. These robust inhibitory responses were easily detected without two-point stimulation, which would likely reveal even more pervasive inhibitory surrounds (Gardner and Constanzo 1980; Laskin and Spencer 1979). The mechanisms for generating these inhibitory surrounds could include direct inhibition or disfacilitation, i.e., inhibition of excitatory neurons that project to the neurons under study.

The difference between the continuous receptor sheet on the mole nose and the discrete receptor arrays on the rat’s vibrissae pad probably accounts for some of the differences in surround receptive fields between the two species. Each whisker is associated with a receptor complex where contact is likely to evoke a response primarily at a single cortical locus. Each star appendage on the other hand is a continuous sheet of receptors and different locations on the appendage activate different areas of cortex. Thus the determination of “where” contact is made in the two systems is necessarily expected to be different.

In the whisker system, the particular whisker or whiskers (Sachdev et al. 2002) that make contact are likely to provide sufficient information about point of contact, whereas on the mole’s star, the where variable can be fractionated into subsections of an appendage. We also know from observing star-nosed mole behavior (Catania and Kaas 1997) that the star is used to discriminate very small prey items that may be only a millimeter in diameter. Objects of this size would often stimulate only a single star appendage. In contrast, rodents seem more likely to integrate information from multiple whiskers as they explore larger objects in their environment.

The small receptive fields and inhibitory surrounds found for the cortical representation of the star seem consistent with the where aspect of perception. At this stage it is more difficult to attribute specific responses to the what aspect of perception. This is perhaps not surprising given the complexity of the star-nosed mole’s somatosensory system. The primary somatosensory cortex (S1) is only one of three relatively large interconnected cortical areas, each of which contains a histologically visible representation of the star (Catania 2000). At present little is known about neuronal activity in these additional areas or how primary afferent activity may be transformed in subcortical stations. However the advantages provided by the multiple large, histologically visible representations of the star appendages may provide a convenient system for further investigations of neuronal activity patterns across multiple sensory areas.

We thank Dr. Ford F. Ehner (Vanderbilt University) for the use of physiology facilities and F. Remple for comments and suggestions on the manuscript.

This work was supported by National Institute of Mental Health Grant MH-58909 to K. C. Catania and by the Searle Scholars Program.

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STAR-NOSED MOLE SOMATOSENSORY CORTEX