

sample correlations were drawn from the same population (12). The χ^2 statistic divided by its degrees of freedom has an expectation equal to 1.0 under the homogeneity hypothesis and can be used to compare the relative heterogeneity of different categories.

Detailed information about the data presented here and a list of studies included and excluded are available from the authors.

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Modular Segregation of Functional Cell Classes Within the Postcentral Somatosensory Cortex of Monkeys

Abstract. *The distribution of two functionally distinct cell types, presumably related to slowly and rapidly adapting mechanoreceptors in the skin, was explored within the representation of the glabrous hand in area 3b of the somatosensory cortex of monkeys. The two cell classes lie in relatively segregated alternating anteroposterior bands within the middle layers of the cortex.*

One of the most basic and fundamental concepts of how the brain is organized is that the major subdivisions—the cortical areas and subcortical nuclei—are further divided into partially isolated local circuit units or modules of neurons united by a common task. This concept was first formalized when Mountcastle (1) proposed that the somatosensory cortex is divided into a mixture of different types of narrow vertical columns, 0.5 mm or less in diameter, extending perpendicularly through the cortical layers. Each column was characterized by neurons having similar overlapping receptive fields on the body surface and responsiveness to a single submodality of somatosensory stimulation. It was suggested that a single or small group of thalamocortical fibers, activated by a single type of peripheral stimulation (such as joint rotation, manipulation of "deep" body tissue, hair movements, or pressure on the skin) at a single body location in turn activates a narrow vertical column of cells, and that adjacent cortical columns are activated by different types of stimulation. The observations that led to this formalization were that vertical microelectrode penetrations in the somatosensory cortex of cats con-

sistently encountered cells responsive to the same submodality of somatosensory stimulation and had overlapping receptive fields. Slanting electrode penetrations, however, revealed short progressions of neurons activated by one submodality interrupted by short progressions of neurons activated by another submodality, as well as shifts in receptive field locations. Such observations have been made repeatedly by many investigators for cortex responsive to sensory stimuli, and there is wide agreement that the sensory cortex is organized into "columns" or "modules." The question that remains is, How is any particular cortical area divided into columns? More specifically, What are the types of columns, what are the sizes and shapes of these columns, and how do the different types of columns relate to one another?

The region of the cortex where this question has been best answered is the striate cortex (area 17) of monkeys, where the precise distributions of ocular dominance columns and orientation columns have been demonstrated (2). In regions other than the striate cortex, investigations of modular organization have been hindered to some extent by a

lack of detailed knowledge of how sensory surfaces are represented in the particular cortical region (3). Until recently, for example, the postcentral somatosensory cortex of monkeys containing the four architectonically distinct zones—areas 3a, 3b, 1, and 2—was thought to contain a single representation of the body and a complex mixture of somatosensory submodalities. It now appears that each architectonic field constitutes a separate representation of the body receiving input from a limited subset of peripheral receptor types (4, 5). Area 3a seems to receive thalamic input related to muscle receptors, and area 2 is activated by thalamic input related to joint and other deep body receptors. Areas 3b and 1 each form detailed topographic representations of the body surface, and each appears to be exclusively or nearly exclusively activated by various types of cutaneous receptors.

Because the somatotopic organizations of areas 3b and 1 are now known in detail, it is possible to perform experiments designed to reveal the modular organization of these areas. Our limited start in this direction has been to explore systematically all of the cortex in area 3b devoted to a single finger of the hand to see how neurons activated by particular receptor types are distributed. We hoped that an understanding of how these inputs are represented in the cortex devoted to the glabrous skin of a single finger would generate a testable hypothesis of how these inputs are organized throughout area 3b.

The two basic receptor types in the skin of primates are slowly adapting (SA) receptors, which respond tonically to a maintained indentation of the skin surface, and rapidly adapting (RA) receptors, which respond phasically only at the onset and offset of applied steady stimuli (6). Our mapping studies revealed that areas 3b and 1 of monkeys contain input from both classes of receptors. We found two types of neurons (Fig. 1A). Both types have phasic responses at stimulus onset and often at offset; one type also has tonic responses while a stimulus indents the skin for a maintained period of time. This type of neuron must receive significant input from peripheral SA receptors and is termed an SA cortical neuron. The other type can be most easily related to RA receptors and is termed an RA cortical neuron. In detailed single and multiple unit studies of the representation of the glabrous hand digits in area 3b, we have found that SA and RA neurons are grouped separately in largely anteroposterior

bands. The skin surface also appears represented separately in the context of each cell type.

Experiments were performed on six owl monkeys (*Aotus trivirgatus*) and nine cynomolgus monkeys (*Macaca fascicularis*) (7). Similar results were obtained from both species. The experimental approach was to characterize the response mode of neurons as SA or RA in a closely spaced grid of penetrations perpendicular to the cortical surface and covering all of the representation of the glabrous skin of a single digit. The representation of digit 3 or 4 was usually chosen for study. Typically, individual

electrode penetrations were spaced 100 to 200 μm apart, and recordings separated by as much as 200 μm in depth were made in each penetration. Most recordings were from single neurons, but in order not to omit recording locations, multiunit responses were recorded whenever single units could not be fully isolated. Receptive fields were defined carefully and noted at every recording site, and peristimulus time histograms were obtained to yield an objective measure of neuron response type.

The first important observation was that individual perpendicular electrode penetrations encountered either only RA

neurons or largely SA neurons. In SA penetrations, SA cells were found predominantly in the middle layers of cortex, presumably close to the thalamic input. However, neurons without any obvious SA component were also found in the SA penetrations, usually above and below the middle layers. In RA penetrations, only RA cells were found regardless of recording depth, but neurons were most easily driven in the middle cortical layers. Thus, it appears that SA and RA thalamic inputs are segregated as they terminate in the middle layers of the cortex and that SA properties are not always detected in neurons above and below the region of direct SA input.

The second important observation was that SA and RA penetrations were not randomly distributed across the cortex, but were clustered together to form slowly adapting and rapidly adapting cortical bands similar to ocular dominance or orientation bands in the striate cortex (2) or summation-suppression bands in the primary auditory cortex (3). The bands tended to extend in a rostral-to-caudal direction, in the same direction as the glabrous surfaces of the fingers are represented from distal to proximal on the cortex.

The arrangement of the slowly and rapidly adapting bands in the cortical representation of digit 4 in area 3b of an owl monkey is shown in Fig. 1. Details of the representation of area 3b representing the glabrous digits of the hand, along with that of the rest of the body, are available elsewhere (4, 5). Figure 1D can be viewed as a slice through the middle layers of cortex parallel to the cortical surface, showing the modular segregation of two functional cell classes. The exact positions of the SA and RA bands vary in the representations of particular digits in individual animals. In Fig. 1D, one SA band is flanked by two RA bands within the representation of digit 4. Other patterns observed have been separate SA bands predominantly at the edges of a digit representation and an RA band in the center and a central SA band bifurcating and flanking an RA band. Bands appear to be continuous across the representations of adjacent digits. The SA bands are narrow caudally but flare out rostrally where the distal phalanx and digit tip are represented. The SA and RA band widths vary from 200 to 600 μm .

The entire digit skin appears to be separately represented by RA and SA cells, as judged by receptive field size and overlap. In Fig. 1D, for example, SA cells had large receptive fields on the proximal and middle phalanges—on the

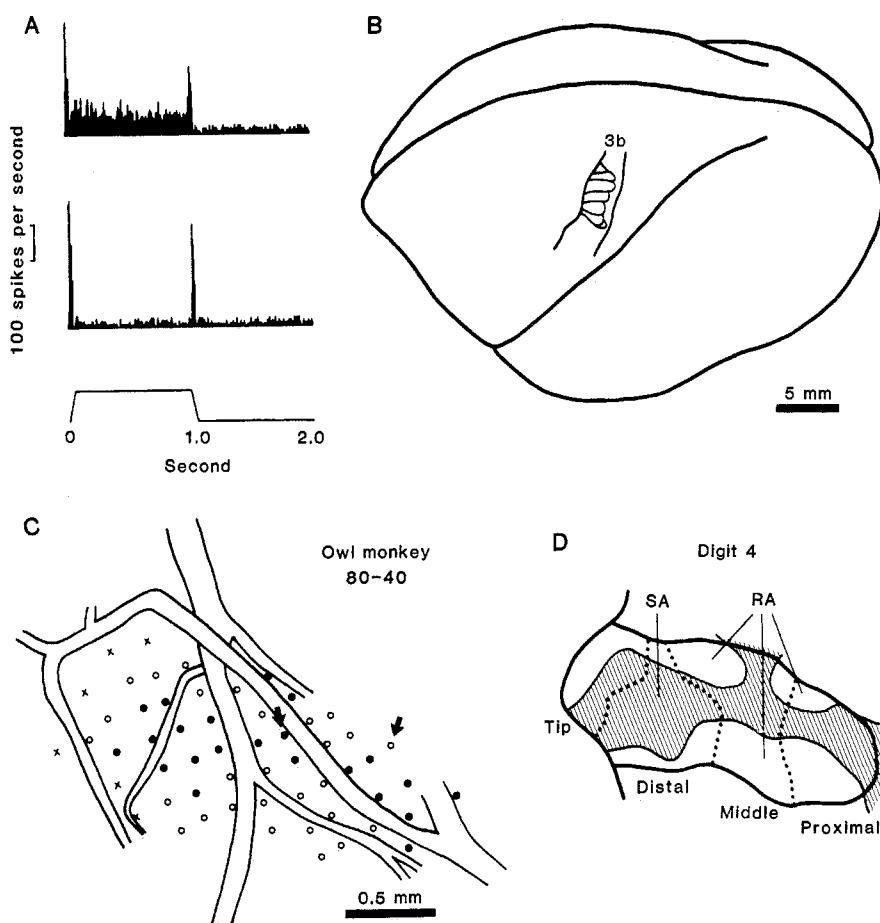


Fig. 1. (A) Peristimulus time histograms obtained from two types of neurons in area 3b of the somatosensory cortex, which is presumed to receive slowly adapting (top) and rapidly adapting (middle) receptor input. Trace at bottom shows waveform of stimulus application. Indentation depth, 700 μm ; rise and fall times, 25.5 msec; indentation time, 1 second. Both cell types show high rates of discharge at stimulus onset and offset and a brief period of suppression of activity afterward. The SA cell also exhibits a tonic discharge through the duration of stimulus indentation. Histogram bin width, 5 msec; 25 stimulus cycles. (B) Hand representation within area 3b of somatosensory cortex in the owl monkey. Digits 1 to 5 are represented in order from lateral to medial. Shaded areas show representation of the dorsal finger skin. Digit tips are represented at the rostral border of the representation, while proximal portions lie progressively caudal. (C) Electrode penetrations within and around the digit 4 representation in area 3b of owl monkey 80-40. Closed circles denote SA penetrations and open circles denote RA penetrations. Crosses denote penetrations in which cells were not activated by cutaneous stimuli and demarcate the border of area 3b from area 3a. Arrows denote penetrations in which the SA and RA neurons of (A) were recorded. Some large blood vessels in the region are shown for reference. (D) Representation of digit 4 obtained from penetrations in (C). Regions represent the digit tip; the distal, middle, and proximal digit phalanges; and the regions of SA and RA cells within the middle cortical layers.

order of an entire phalanx—whereas RA cells had smaller receptive fields—on the order of half a phalanx in size. Field centers for SA cells on the proximal and middle phalanges were centrally located on the digit, whereas those for RA cells favored the radial and ulnar aspects of the digit. Receptive fields for RA cells, however, overlapped the central portion of the digit. Within the distal phalanx and digit tip representation, in contrast, the receptive fields for SA cells were smaller than receptive fields for RA cells. An inverse relation between receptive field area and cortical area of representation, which held generally over larger regions of the area 3b representation (8), also seemed to hold within the finer organization of the area 3b map.

We regard these observations as an important step in the understanding of the modular organization of the somatosensory cortex. In a sense, the four architectonic strips 3a, 3b, 1, and 2 constitute the initial functional subdivisions of the somatosensory cortex, each receiving different submodal inputs systematically from the entire body surface. This study suggests that area 3b receives predominantly cutaneous input (9) and is further divided into alternating bands of neurons related principally to the SA and RA cutaneous receptor types. The skin surface is represented separately by the neurons in each functional class. We have shown previously that the cortical area that would represent a point on the skin within the area 3b representation in owl monkeys is 500 to 600 μm in diameter (8). The dimensions of SA and RA bands obtained in this study are consistent with the hypothesis of a point's being subserved by both afferent types. Alternately, the cortical area that would represent a region of skin the size of a receptive field is 1 to 1.2 mm in diameter. Such an area would contain approximately one set of adjoining SA and RA bands. This concept of cortical organization for area 3b of primates is directly analogous to the concept of ocular dominance columns being combined in "hypercolumns" in area 17 of monkeys (2) and does not preclude the existence of other segregated features of cortical organization in area 3b such as the orientation columns in area 17.

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Human Homing: An Elusive Phenomenon

Abstract. Recent experiments suggest an ability of blindfolded humans transported from home to indicate the direction of displacement. Attempts to replicate these results have been unsuccessful.

Baker has recently reported experiments that indicate an ability in humans to navigate without instruments or celestial cues (1). Baker transported blindfolded high school and college students in buses and vans over indirect routes to "release" sites 6 to 52 km away and asked them, while they were still blindfolded, either before or after they left the van, to name or write down their estimate of either the compass direction of home or of the site from home. The students were moderately accurate in their estimates, displaying a mean error of only 47° (compared to 90° to be expected on the basis of chance alone), with mean vector lengths (a measure of the degree of consistency of estimates between subjects) in the range of 0.38 to 0.75 (where 0.0 indicates complete randomness and 1.0 represents perfect agreement). The possibility of such distributions arising by chance is less than 1 percent. Curiously enough, the ability of his subjects actually to point in the homeward direction or write down the direction of travel on any individual leg of the journey was only marginal; and on journeys with multiple stops, individuals who were poorly oriented at, for example, 10 km were as likely to be correct at 15 and 20 km as that subset which had been well oriented earlier (2). Baker also found that the accuracy of naming or writing the homeward bearing was reduced if his subjects wore magnets rather than equivalent weights on their blindfolds.

In view of the exciting nature of these results, we have tried on eight separate occasions to repeat Baker's experiments (3). In the first attempt, 40 Princeton undergraduates (essentially all of whom

had lived in Princeton for at least 2 years) wearing double-layered velour blindfolds and black felt hoods were transported in a school bus and two vans, whose windows were covered with aluminum foil to reduce solar cues, over a circuitous path (route 1 in Fig. 1) to a location 20 km from Princeton (site 1 in Fig. 1). Half of the students wore alnico magnets attached to their blindfolds approximately between their eyes—very near the site proposed by Baker for a human magnetic sense organ (2)—while the others wore equivalent weights. The magnets produced fields at least as strong as those used by Baker, and, as in Baker's experiments, both magnetic polarities were used. The two groups were kept segregated to avoid any effects the magnets might have on the control subjects, and no one knew whether they wore magnets or weights. The students wrote down their estimate of the compass direction of home. The mean vector of the control group was 98° left of home, and the orientation was not statistically significant (Fig. 1). The mean vector of the magnet wearers (data not shown) was more accurately directed—12° to the right of the homeward bearing—although the mean vector length of 0.27 was again not statistically significant. Pointing was also random: a mean vector of 0.14 at 78° left for controls and 0.10 at 42° left for those with magnets. There was no effect of being transported in a van compared to the bus, nor was there any effect of seating position in either type of vehicle. These results provide no support for the hypothesis that humans can determine the direction of displacement or sense the earth's magnetic field.

The second test involved 15 graduate