

Receptive fields of neurons in areas 3b and 1 of somatosensory cortex in monkeys

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Receptive fields of neurons within the separate representations of the glabrous hand in areas 3b and 1 of somatosensory cortex were studied in cynomolgus monkeys. Many neurons in area 1 have center-surround receptive fields with separate 'on' and 'off' zones, while neurons in area 3b exhibit largely uniform or homogeneous receptive fields.

In a set of landmark experiments, Mountcastle and Powell⁸ first systematically investigated the properties of neurons in postcentral somatic cortex in monkeys. One feature of receptive fields they described was the existence of separate excitatory and inhibitory regions on the skin for some cells in areas 3b and 1 receiving cutaneous input. Since then, other properties of postcentral somatosensory neurons with cutaneous receptive fields, such as selectivity to direction of stimulus motion^{2,4,17} and to orientation of an edge^{4,13} have been described. However, detailed study of some important aspects of receptive field organization, such as antagonistic subregions within receptive fields, has been curiously neglected since the initial experiments of Mountcastle and Powell. Such studies seem especially important now in the light of the recent discovery that the separate architectonic fields, 3b and 1, of postcentral 'SI' cortex of monkeys each contains a complete and separate representation of the contralateral skin surface^{5,6}. It seems reasonable to suppose that each of these separate representations has a different functional role, and that these different functional roles will be reflected in the properties of the neurons within the representations. A number of observations on the nature of afferent input, patterns of anatomical connections and the behavioral effects of cortical lesions support these hypotheses (see ref. 6 for review), but direct comparisons of neurons representing the same body region in the two cortical fields are needed. This report describes some initial results from ongoing experiments aimed at defining the functional properties of cells in areas 3b and 1 of somatosensory cortex in macaque monkeys. For neurons with receptive fields located on the glabrous hand, many neurons in area 1 have receptive fields that exhibit a center-surround organization with separate 'on' and 'off' zones, while neurons in area 3b exhibit largely uniform or homogeneous receptive fields.

Data reported here were obtained from 12 experiments on 6 cynomolgus monkeys (*Macaca fascicularis*). Animals were anesthetized with ketamine HCl (25

mg/kg, i.m.; supplemented as needed). In 8 experiments, recordings were made through a plexiglass chamber cemented over a trephine hole in the skull. The dura was reflected and Pt-Ir electrodes used to make penetrations that either lay within the caudal part of area 1 exposed on the postcentral gyrus or passed down the posterior bank of the central sulcus through rostral area 1 and most of area 3b. A 3% solution of agar in the chamber, which was topped with dental wax, provided stable recordings of extracellular membrane potentials. In 4 experiments, electrodes were angled either posteriorly, and penetrations made through motor cortex so as to intersect portions of areas 3b and 1 buried in the central sulcus¹⁵, or laterally, and penetrations made at the posterior lip of the central sulcus so as to traverse considerable distances along cortex in the posterior bank of the sulcus. The palm of the animal was embedded in plasticene. After a unit was chosen for study, a rough receptive field determination was first made using a hand-held glass probe. A set of peristimulus-time (PST) histograms were then obtained on-line, with step indentations provided by an electromechanical stimulator¹, at different positions inside as well as outside the receptive field. Stimulus positions were usually equidistant and spaced 2–3 mm apart. All stimulus parameters were kept constant for each receptive field delineation. Indentation depths were 500 or 700 μm for individual fields. In intensity series that were done on 2 slowly adapting (SA) cells (see below), such indentation depths were found to lie intermediate between threshold and saturation. Similar observations have been made in rhesus monkeys for SA cells in cortex⁷ and in SA primary afferent fibers³. While receptive fields were mapped using one stimulator at many positions, for some receptive fields a second, hand-held, probe was used in addition to stimulate separate positions on the skin surface and test for inhibition of cell responses.

Electrode tracks and lesions made in terminal experiments were identified later in sagittal sections. Cells could be reliably assigned to either area 3b or 1 on the basis of track reconstructions, by relating depth from cortical surface to architectonic borders, and by relating locations of receptive fields within the two representations to a prior detailed map of the hand region¹⁰. While the laminar locations of cells were not precisely determined, nearly all cells were judged to be recorded from the 'middle' layers of cortex, laminae III, IV and V.

Two types of cells could be clearly distinguished in areas 3b and 1 on the basis of their responses to a step indentation. Both had phasic responses to stimulus onset and offset. One type of cell also had tonic responses during the maintained indentation; these were termed slowly adapting (or SA, e.g. histogram 1, Fig. 1). The other type of cell exhibited only the transient responses; these were termed rapidly adapting (or RA, with PST histograms like 7, Fig. 1). The definitions for SA and RA cells used here follow those used previously for primary afferent fibers¹⁶ and somatosensory cortex^{11,12}. Often the transient responses of both SA and RA cells at stimulus onset and offset were followed by a relative suppression of activity (of duration 25–150 msec) and then a recovery to the appropriate rate of discharge.

Sixty-seven cells in area 3b (13 SA, 54 RA) and 60 cells in area 1 (5 SA, 55 RA) were classified for receptive field organization. Cells receiving Pacinian receptor input, known to lie within area 1^{6,9}, were noted but not studied. Receptive fields were

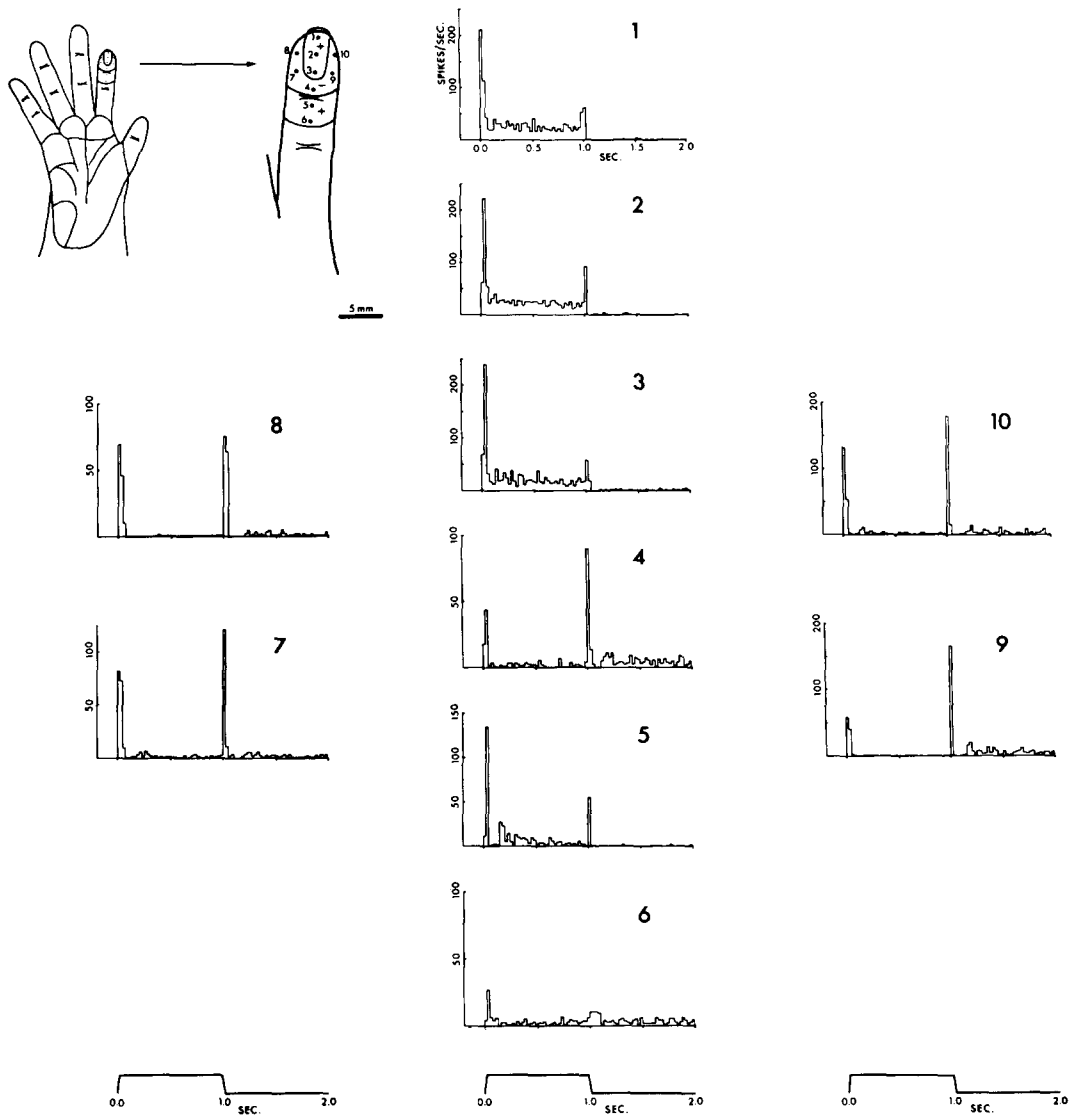


Fig. 1. 'On'-center 'off'-surround receptive field of a slowly adapting cell recorded in area 1. Top, left: 10 stimulus positions within the receptive field on digit 2. Middle: PST histograms obtained at the corresponding stimulus positions. Fifty stimulus cycles; bin width, 25 msec. The receptive field has a core 'on' zone (positions 1,2,3) surrounded by an 'off' zone (positions 4,7,8,9,10) and a relatively weak 'on' outer surround (positions 5,6). Bottom: stimulus waveform used for constructing histograms. Indentation time, 1.0 sec; rise and fall times, 25.5 msec; indentation depth, 700 μ m.

classified as homogeneous or center-surround based on their responses during stimulus 'on' and 'off' times in different portions of the fields. 'On'-center 'off'-surround receptive fields had field centers with higher proportions of 'on' to 'off' responses both at the core center itself as well as with respect to the surround, and

surrounds with higher 'off' than 'on' responses (Fig. 1). 'Off'-center 'on'-surround fields were of the opposite type. Homogeneous receptive fields had similar ratios of 'on' to 'off' responses throughout the field.

Fig. 1 illustrates the organization of an 'on'-center 'off'-surround receptive field recorded from a SA cell in area 1, approximately 1200 μm from the cortical surface. The receptive field, largely on the distal phalanx of digit 2, had a core excitatory zone from which clearly SA responses were obtained (stimulus positions 1, 2 and 3). Surrounding this core zone on three sides was a belt where 'off' responses were larger than 'on' responses. Stimulus positions 4, 7, 8, 9 and 10 illustrate that not only was the transient response to stimulus offset higher in the surround, but there was a sustained 'off' component to the response too. In all histograms in Fig. 1, the first bin after stimulus application or removal contains essentially the entire response during the onset or offset time. At several stimulus positions, however, the phasic response at stimulus onset or offset was seen to persist for some time after the stimulus probe had ceased to step in or out of the skin. These responses show up in the one or two bins following the first bin at stimulus application or removal. At positions 4, 8, 9 and 10, not only the response in the initial bin but also the entire phasic response at offset was higher than that at onset. The surround was asymmetric in that it did not extend over the distal portion of the center. The receptive field further exhibited a diffuse excitatory outer surround, illustrated by stimulus positions 5 and 6.

The effect of the 'off' surround on the 'on' center is documented in Fig. 2. The stimulus probe, set up at position 1 of Fig. 1, indented the skin for 20 sec. During the stimulus 'on' period a hand-held glass probe was applied to the surround 5 sec after the start of the center stimulus for a period of 6 sec. It is evident that the surround had a strong inhibitory effect on the center, for the cell was shut down almost completely.

Unlike the 'on'-center 'off'-surround receptive field of the SA cell shown in Fig. 1, SA cells with homogeneous receptive fields recorded in areas 3b and 1 had similar responses at several stimulus positions across their fields. All SA cells with homoge-

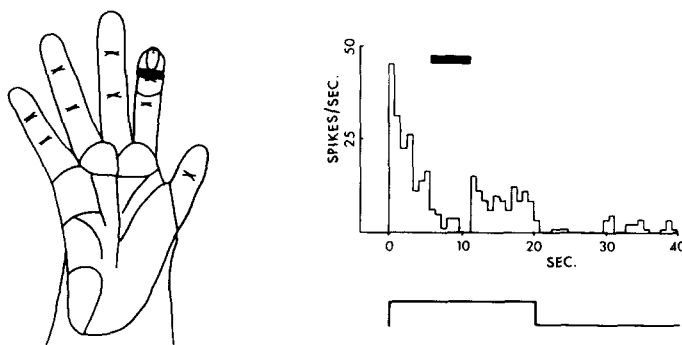


Fig. 2. Effect of the 'off'-surround on the 'on'-center for the receptive field shown in Fig. 1. Dot in the field center shows excitatory stimulus position (same as 1, Fig. 1). Excitatory stimulus waveform shown below PST histogram. Dark bars in the field surround and above histogram show place and time of application of a second, inhibitory stimulus. PST histogram bin width, 800 msec; 1 stimulus cycle.

neous receptive fields had higher phasic 'on' than 'off' responses throughout their fields, and of course higher tonic responses (the maintained discharge, if any, during stimulus 'off' being the background discharge of these cells). Usually thresholds for tonic responses obtained from a SA cell rose somewhat in moving away from the central portion of its receptive field, i.e. for stimulus positions away from the central region higher indentations were required to elicit the same level of tonic responses that could be obtained by lower indentations at the central portion. However, homogeneous receptive fields of SA cells could be reliably classified due to the basic similarity of their 'on' and 'off' transient and sustained responses to stimulation at all positions. All 13 SA cells recorded in area 3b and 4 (of 5) SA cells recorded in area 1 had homogeneous receptive fields.

For RA cells, the receptive field classification was based on the magnitude of only the phasic responses elicited at stimulus onset and offset. All 54 RA cells in area 3b had homogeneous receptive fields. Two of these cells had larger 'off' than 'on' responses throughout their receptive fields. Thirty-eight RA cells in area 1 had homogeneous receptive fields. All of these had higher proportions of 'on' to 'off' responses throughout. Seventeen RA cells in area 1 had center-surround receptive fields; 11 of these had 'on' centers and 'off' surrounds while 6 had 'off' centers and 'on' surrounds. RA cells with similarly organized center-surround receptive fields were often found in small clusters within area 1. Antagonistic surrounds of receptive field centers that were away from a finger tip were usually symmetrically placed around the center. Surrounds of receptive field centers located at a digit tip were asymmetrical and situated proximal to the centers on the glabrous skin only (e.g. Fig. 1).

The present report describes center-surround receptive fields for cells receiving input from the glabrous skin of the hand, based on responses at stimulus 'on' and 'off' times at different receptive field positions. Other studies have demonstrated excitatory and inhibitory zones within receptive fields of cells in postcentral somatosensory cortex of monkeys, for the hairy skin of the limbs and trunk^{8,17}. One issue that becomes important in comparing results from different studies is the definition of 'off' as compared to 'inhibitory' zones¹⁴. Delineation of an 'off' zone in this report is based on an excitatory response to stimulus removal. An 'inhibitory' zone of a receptive field is a region of skin that, when stimulated, reduces the cell's spontaneous discharge or the response being elicited from the 'excitatory' zone. Delineation of an 'inhibitory' zone is therefore based on inhibiting a cell's response by stimulus application. It follows that an 'off' zone can be different from an 'inhibitory' zone; however, the two sets of definitions generally coincide for receptive fields classified as center-surround in the present sample (e.g. Fig. 2).

One possible source of the transient as well sustained 'off' response would then appear to be release of inhibition following stimulation of an 'off' zone. Another conceivable source of at least the transient 'off' response elicited from SA cortical cells may be convergent input from some RA afferents on central 'SA' cells. 'Off' responses at stimulus offset have not been described for SA type I or type II cutaneous afferents, while RA primary afferents do exhibit such discharges¹⁶.

About one-third (18 of 60) of the cells recorded in area 1, and none of the cells

recorded in area 3b ($n = 67$), exhibited center-surround receptive fields. All cells recorded within areas 3b and 1 had receptive fields located on similar skin surfaces, glabrous digits 2, 3 or 4, within the separate representations in the two areas. The sample of cells, however, may not be entirely representative of all cells in areas 3b and 1. An important factor probably related to receptive field organization is the laminar location of cells. It is possible that some cells superficial or deep to the middle layers of cortex recorded exhibit an antagonistic receptive field organization in area 3b, and that larger proportions of similarly situated cells do so in area 1. Mountcastle and Powell⁸ found cells with excitatory and inhibitory regions in area 3b. Experiments on correlating receptive field type with lamina are in progress.

A second factor that may affect the numbers of cells classified as possessing center-surround receptive fields is the anesthetic used. Barbiturates affect temporal and spatial inhibition in somatosensory cortex (e.g. ref. 8). Effects of ketamine HCl on response properties of cells were not studied systematically in the present experiments, although dramatic effects on cell responses during and following administration of supplementary doses of anesthetic were not observed. Yet it remains possible that the anesthetic does mask center-surround receptive field properties of some neurons in areas 3b and 1. However, unless area 3b cells are affected preferentially by ketamine HCl, area 3b appears to differ from area 1 in the numbers of neurons that exhibit center-surround receptive fields on the glabrous hand.

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