

THE VISUAL CLAUSTRUM OF THE CAT

III. Receptive Field Properties¹

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Abstract

The visual response properties of cells in the cat's dorsocaudal claustrum were studied physiologically. Quantitative observations were made on 55 cells, and qualitative observations were made on 228 others.

The claustral cells formed a physiologically homogeneous population. The overwhelming majority were orientation selective, and most also showed a striking preference for long stimuli, their responses summing up to lengths of 40° or more. Moving stimuli were always much more effective than stationary ones. In other respects, claustral cells were tolerant of wide variation in stimulus features. Their responses were about equally brisk to either direction of movement of a properly oriented stimulus, and the velocity of movement was likewise not critical. They appeared not to summate across the dimension of their receptive fields orthogonal to the preferred orientation so that narrow or broad slits, or edges, evoked similar responses. Dark slits on light backgrounds were as effective as light slits on dark backgrounds. Finally, a large majority of cells were driven equally well by either eye. These properties of claustral cells differ in several respects from those of their principal targets, cells in layer IV of visual cortex.

In the first two papers of this series, we examined the connections and visual field topography of the cat's visual claustrum (LeVay and Sherk, 1981a, b). These experiments indicated that it is linked almost exclusively to the visual cortex and contains an orderly map of the contralateral hemifield. The present paper investigates the receptive field properties of single claustral cells.

Early single unit studies suggested a rather diffuse organization within the claustrum, with an intermingling of different sensory modalities (Segundo and Machne, 1956; Azzaroni et al., 1968a, b; Spector et al., 1970, 1974). The first physiological suggestion of a functional parcellation within the nucleus was the report by Rapisarda et al. (1969) that visually evoked potentials could be obtained most readily in the dorsocaudal part of the claustrum.

Our work (LeVay and Sherk, 1981b) and the concurrent experiments of Olson and Graybiel (1980) confirm that cells in this part of the claustrum are visually responsive, while Olson and Graybiel have delineated, in addition, auditory and somatosensory regions with physiological methods.

In the present study, we have found responses in the dorsocaudal claustrum to be exclusively visual. In terms of their receptive field properties, cells in this region form a rather uniform population, and in several respects, particularly in their orientation selectivity, they resemble visual cortical neurons. Their most striking property is a preference for very long slit stimuli. Under "Discussion," we take up the problem of how claustral cell properties might relate to those of their cortical afferents and to those of their cortical targets.

Materials and Methods

Response properties of single units were studied in 14 cats. The methods of preparing the animals and recording have been described in the first paper of this series (LeVay and Sherk, 1981a). These experiments generally lasted about 24 hr.

In six of these cats, visual responses were measured quantitatively. An optic bench was used to generate slits of light, in conjunction with a waveform generator and a Scanner Control (General Scanning, Inc.) that swept the slit prismatically. Spikes were passed through a window discriminator whose output was fed into a computer of average transients (CAT, Technical Instruments Inc., North Haven, CT). The latter also triggered the stimulus sweep and displayed histograms of cell responses during 10 to 20 stimulus sweeps. The histogram duration was 8 sec, and spikes were collected into 200 bins each 40 msec

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long. Sweep velocity could be varied from 4.5 to 112°/sec, while the sweep length was held constant at 35°. Histograms were photographed from the cathode ray tube screen of the CAT for later analysis. Spontaneous activity was counted during the interval between stimulus sweeps across the receptive field. In some experiments, we used a spike counter built into the window discriminator to count responses to individual stimulus sweeps, which gave us information on response variability.

The pattern of stimulus-dependent activity in the claustrum was studied in one cat using the 2-deoxyglucose method of Sokoloff (1975), modified according to Livingstone and Hubel (1981). This experiment was performed by D. Hubel and M. Livingstone (Department of Neurobiology, Harvard Medical School), and the sections containing the claustrum were kindly made available to us. The cat was anesthetized, placed in a stereotaxic frame, and paralyzed, and its eyes were refracted and aligned as if for physiological recording. An intravenous injection of 2-[¹⁴C]deoxyglucose was given over 5 to 10 sec, and then the cat was stimulated binocularly for the following 45 min. The stimulus consisted of a pattern of vertical stripes covering a portion of the left hemifield from about 2° to 22° away from the vertical meridian. The stripes were graded in width, ranging from ¼° near the midline to 2 to 3° in the periphery; they were moved continuously at about 2°/sec. The vertical meridian and right hemifield were illuminated diffusely. The cat then was given an overdose of Nembutal and perfused with 10% formol-saline, and the brain was removed and frozen at once to -100°C in Freon 25 cooled with liquid nitrogen. Subsequently, 30- μ m sections were cut at -30°C, placed on coverslips, and heated rapidly to 98°C to avoid diffusion of the label. Because of the small size of the claustrum, we used a fine grained film (DuPont Graphic Arts) rather than x-ray film for autoradiography. This, together with the comparatively low level of 2-deoxyglucose uptake in the claustrum, necessitated a relatively long exposure (12 weeks).

Auditory stimuli consisted of hisses, hand claps, clicks, and other broad band sounds. Somatosensory stimulation was carried out by stroking the fur or applying firm pressure. We did not manipulate the animal's joints nor did we test temperature or pain sensitivity.

Results

The great majority of cells in the dorsocaudal claustrum responded to visual stimuli. In early experiments, we also tested all cells with auditory and tactile stimuli (see "Materials and Methods") but failed to obtain any responses to them.

The briskness and reliability of visual responses varied markedly from cat to cat. In two animals, we were unable to study claustral response properties at all because cells were so poorly responsive; in others, the responses of some cells were obscured by extremely bursty spontaneous activity, particularly as the electrode neared the ventral boundary of the visual claustrum. More commonly, however, spontaneous activity was low, and responses were fairly brisk and consistent like those illustrated in Figure 1. In a sample of 53 cells, the median

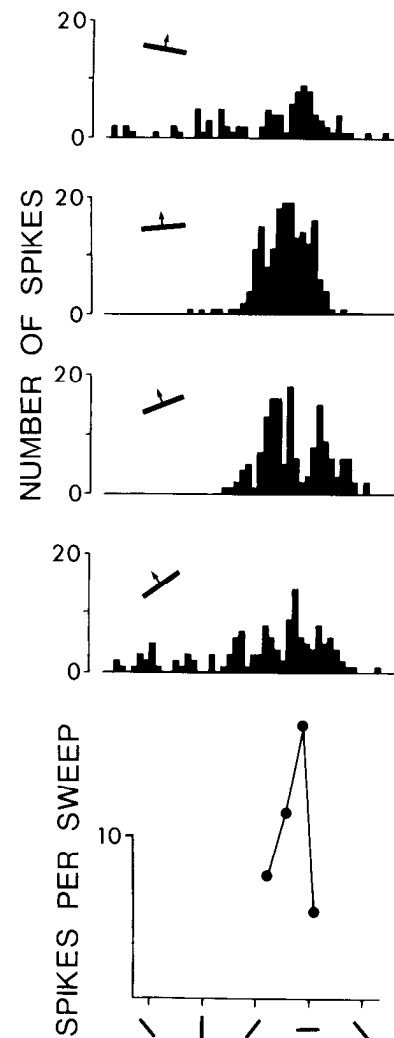


Figure 1. Histograms of a claustral cell's response to four different stimulus orientations. Each histogram sums the cell's responses to 10 sweeps of a 43° slit; the histogram shows a 4-sec segment of the sweep, and spikes have been collected into 50 80-msec bins. To plot the response as a function of slit orientation (*bottom graph*), the number of spikes in each histogram were counted over a 1-sec interval centered on the peak and then divided by the number of sweeps, 10; this measure is called *spikes per sweep* in this and subsequent orientation- and length-tuning curves.

spontaneous activity was 0.7 spike/sec, while the median response to an optimal stimulus, counted over a 1-sec interval, was 13.5 spikes/sec.

An example of a typical claustral cell's responses is shown in Figure 1. This cell was recorded in the right claustrum, and the center of its receptive field was located 27° to the left of and 7° below the area centralis. The shape of its field was remarkable: though only 2° wide, its length parallel to the horizontal meridian was 33° or more. A narrow, nearly horizontal light slit 40° long, moved slowly through this field, elicited a maximal response, averaging 16.5 spikes/sweep (Fig. 1, *second histogram from top*); movement up or down worked equally well. The same slit left motionless in the receptive field and turned on and off elicited only weak and erratic responses. Tilting a moving slit away from horizontal

also drastically diminished the response: a rotation of 19° was sufficient to reduce the response by half (Fig. 1). Equally striking was the effect of shortening the slit. Slits reduced progressively from 40° elicited gradually weaker responses until, at 5° , the response was barely discernible even when averaged over 10 trials. The cell responded equally well through either eye, and it had no spontaneous activity.

Although claustral cells varied in the degree to which they shared these characteristics, they formed a rather homogeneous population; we found no clearly distinct subtypes. We examined quantitatively the visual response properties of 55 cells in six cats and made qualitative observations on 228 other cells; these results are presented below.

Orientation and direction selectivity. Orientation selectivity, generally considered a property unique to visual cortical cells, was found to be an essential characteristic of cells in the claustrum as well. Only 2 out of 69 cells that we studied carefully did not have a preferred orientation. Our impression using hand-held stimuli was that many cells were very exacting in their orientation requirements, so that rotating a slit away from the optimal orientation by 30° or so reduced the response drastically. To measure this quantitatively, we constructed orientation-tuning curves for 54 cells. The tuning curve, which plotted response as a function of orientation, was derived from 4 to 10 response histograms, each based on 10 or 20 sweeps at a given orientation (see Fig. 1). Rather than being interleaved, different orientations were presented successively, a method of analysis that can be affected by short term variations in neuronal responsiveness. Most cells responded quite consistently, however, and the tuning curves appeared to reflect their orientation sensitivities reasonably well. Examples are shown in Figure 2. We measured the half-width at half-height of each curve (the angle through which the stimulus must

be rotated to reduce the response by half) and found that the median value was 27° (Fig. 3), confirming that claustral cells were indeed highly selective for orientation.

All possible preferred orientations were represented in our sample, but, among cells having receptive fields fairly distant from the area centralis (15° or more), there was a weak bias toward the horizontal orientation. We were uncertain whether this bias reflected a real nonuniformity in the cell population or whether it resulted from sampling problems. The latter was a strong possibility because orientation preference seemed to be organized in an orderly fashion within the claustrum, as described below, so that cells recorded successively along an electrode penetration often had similar preferred orientations. Different penetrations, however, should provide independent samples. In order to obtain an unbiased distribution, we therefore chose to represent each penetration by a single preferred orientation, this being the one encountered most commonly in that penetration. Only cells with peripheral receptive fields (at least 15° from the area centralis) were included in the analysis.

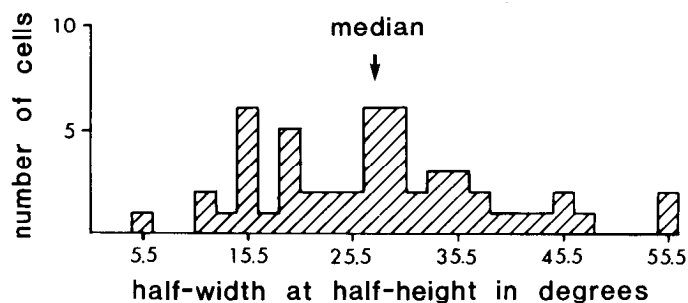


Figure 3. Orientation selectivity measured for 52 cells. Each value is the half-width at half-height derived from orientation-tuning curves such as those shown in Figure 2. The median value was 27° .

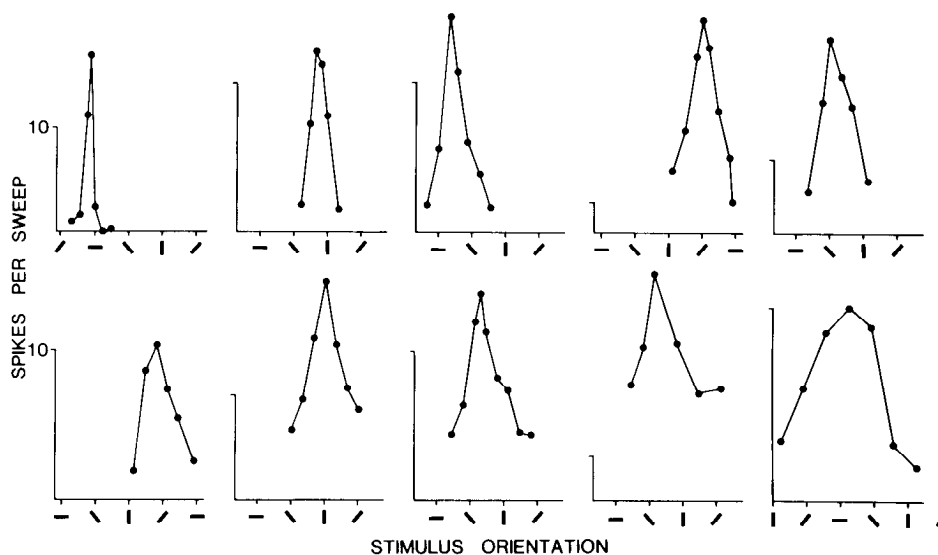


Figure 2. Orientation-tuning curves for 10 claustral cells. These plot the response (as defined in the legend to Fig. 1) as a function of slit orientation. The curves are ordered from most selective to least selective. At the optimal orientation, both directions of movement were tested, and in each case, responses to the two directions were similar, so that only one is shown here. The spontaneous activity of these cells was low.

The resulting histogram (Fig. 4) showed a clear bias toward horizontal.

There were indications of a spatial organization of preferred orientations within the claustrum reminiscent of that described in the visual cortex (Hubel and Wiesel, 1962, 1963, 1974). On vertical electrode penetrations, we frequently encountered sequences of cells having very similar preferred orientations (Fig. 5, *penetrations 1, 4, and 5*). Less commonly, sequences of cells were recorded whose preferred orientations changed in an orderly, around-the-clock fashion as the electrode advanced (Fig. 5, *penetrations 2 and 3*). Abrupt changes in preferred orientation and apparently random sequences were also sometimes encountered. Because only vertical penetrations were made, which did not permit study of sequences longer than about 1 mm, we could not deduce the layout of orientation domains within the claustrum from physiological observations.

To test the idea that cells with similar preferred orientations are grouped together in the claustrum, we counted the number of sequentially recorded pairs of cells (up to 150 μm apart) having preferred orientations within 30° of each other. If the distribution were random, we would expect one-third of all such pairs to meet this criterion. In fact, 137 of 175 pairs, or 78%, did so.

An experiment using 2- ^{14}C deoxyglucose provided additional evidence for the existence of orientation domains and suggested how they might be arranged in the claustrum. A large segment of this cat's left visual field, from about 2° to 22° away from the vertical meridian, was stimulated with long, moving vertical stripes for 45 min following an intravenous injection of 2- ^{14}C deoxyglucose. Coronal sections of the right claustrum processed for autoradiography showed two discrete patches of label (Fig. 6, A to D). The outer margin of the claustrum, which represents the far periphery of the visual field (LeVay and Sherk, 1981b), was unlabeled; this part of the field was not stimulated. Likewise, the unlabeled ventral portion of visual claustrum presumably corresponds to the unstimulated 2° strip along the vertical meridian. The intermediate region contained the heavily labeled patches and more lightly labeled areas between

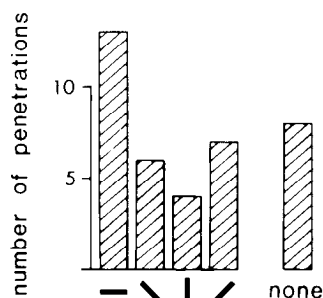


Figure 4. Predominant orientations encountered on 37 electrode penetrations through the claustrum. Only cells with fields beyond 15° eccentricity were considered. For each penetration, the preferred orientations of these cells were grouped into four categories, vertical, horizontal, and left and right oblique. One of these was considered to predominate in a penetration if a plurality of cells fell in this category; otherwise, the penetration was included in the column labeled *none*. Horizontally dominated penetrations were more common than others.

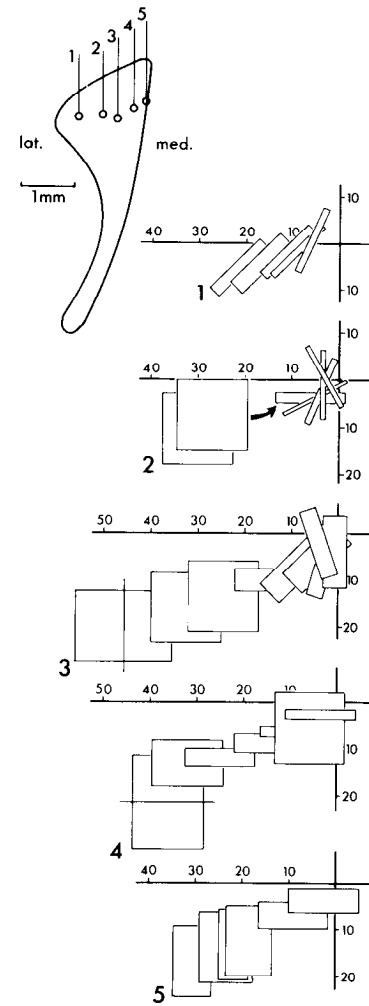


Figure 5. Sequences of receptive fields plotted along five penetrations made in one coronal plane. The first field plotted in each sequence was the most distant from the area centralis, and those encountered subsequently are shown as overlapping their predecessors. Because of the uncertainty in plotting the extreme ends of fields, their lengths are shown arbitrarily as 15° , and those for which we did not find a preferred orientation are shown as $15^\circ \times 15^\circ$ squares. (More detailed study might well have shown these cells also to be orientation selective.) *Penetrations 1, 4, and 5* show sequences of cells with similar preferred orientations. *Penetrations 2 and 3* show gradual counterclockwise rotation of preferred orientations. *lat.*, lateral; *med.*, medial.

them and probably to either side as well. We interpret the labeled patches as being centered on domains containing cells selective for vertical orientations, with the gaps containing cells preferring other orientations. The labeled patches could be followed through many sections until, rostrally, they became blurred and indistinct; near the caudal pole, they became faint and appeared to coalesce into a diagonal band. Through the middle of the anteroposterior extent of the visual claustrum, for a distance of about 1.2 mm, the patches could be traced with some confidence and were clearly continuous, forming two worm-like structures running parallel to the long axis of the claustrum. We are uncertain what happens more anteriorly, where the roof of the claustrum is flat and meets both medial and lateral edges at acute angles.

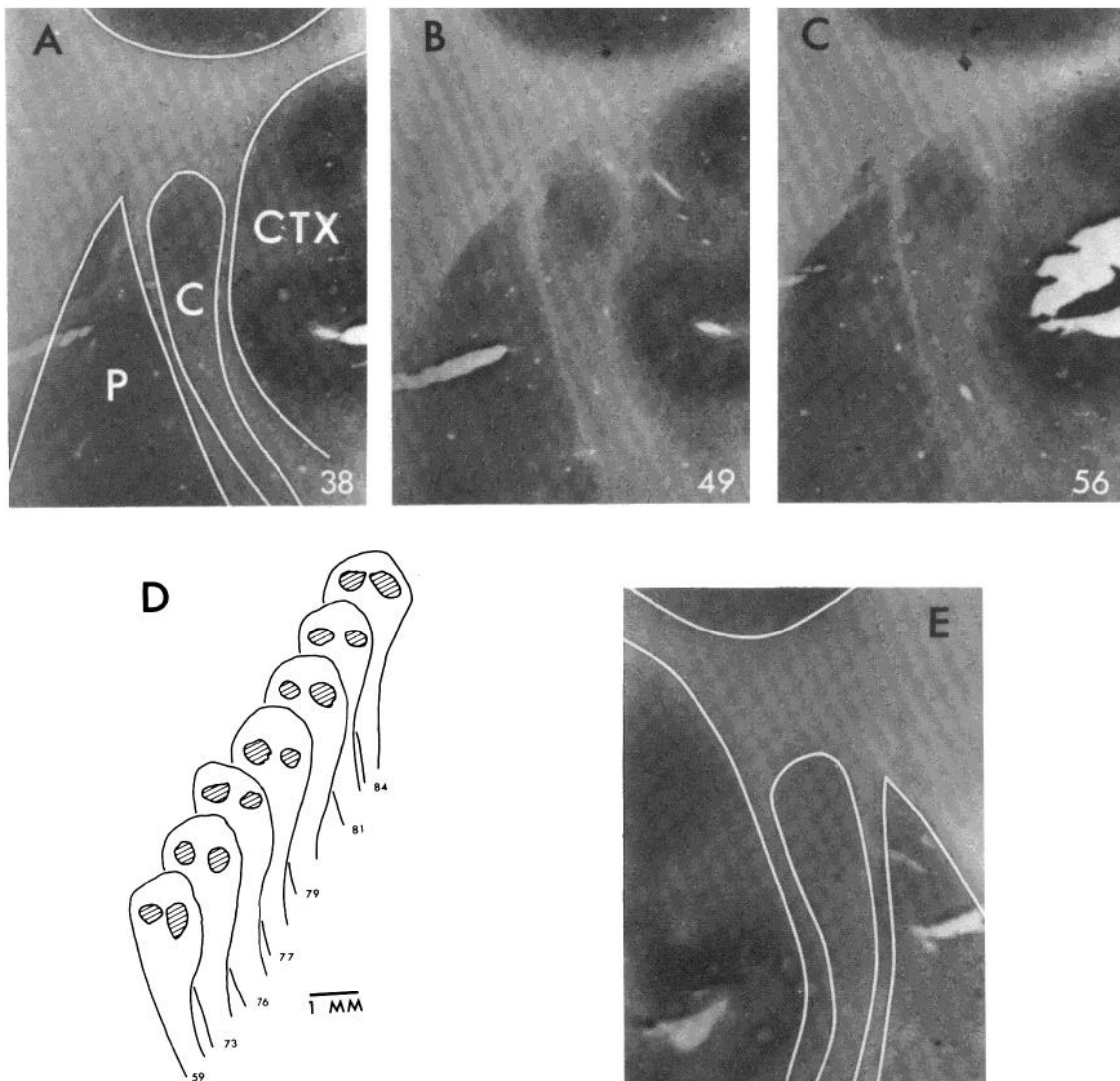


Figure 6. Autoradiographic labeling after a 2- ^{14}C deoxyglucose injection in a cat stimulated in the left hemifield with vertical stripes. **A to C**, Three coronal sections through the right claustrum, seen in light field, showing two dark patches. **C**, claustrum; **P**, putamen; **CTX**, cortex. **D**, A series of claustral sections, each 20 μm thick, spanning 0.52 mm along the long axis of the nucleus from caudal to rostral. Only the sections having the clearest patches were drawn so that the spacing of the series is irregular; *numbers* identify the position of each section in the complete series, which is continuous through *parts A to D* of the figure. The autoradiographs probably exaggerate the size of the vertical orientation domains both because of the limited resolution of the method and because the stimulus excited, though less strongly, cells selective for oblique orientations. **E**, Right (unstimulated) claustrum of the same animal, showing uniform labeling.

The left claustrum, representing the unstimulated right hemifield, was weakly and uniformly labeled (Fig. 6E).

Most cells gave very similar responses to both directions of motion of a properly oriented slit. The ratios of the responses to the two directions, found for 48 cells, were clustered tightly around 1 in a normal distribution (Kolmogorov-Smirnov test) shown in Figure 7. Only 3 cells had a ratio greater than 2:1, generally considered a minimum criterion for direction selectivity.

Length summation and receptive field size. The responses of most cells increased as the stimulus was lengthened, often summing up to the longest slit we tested (43°). We quantified this length dependence for 48 cells by constructing length-tuning curves, and 11

examples are shown in Figure 8. Most of these curves demonstrated a striking degree of summation. The curves for a few cells showed irregular peaks and valleys, which we suspect are artifacts caused by variability in responsiveness. Only one cell showed some decline in its response to longer slits. In order to look at the overall length summation exhibited by claustral cells, we needed an index of summation for each cell; to minimize the problem of response variability, we took the length at which the response reached 75% of maximum on each curve. For 48 cells, this value averaged 15.8° (SD = 9.0° ; range = 4.5 to 39.6°), and the median was 12.5° . We expected the greatest length summation to be shown by cells with the most peripheral receptive fields, but there

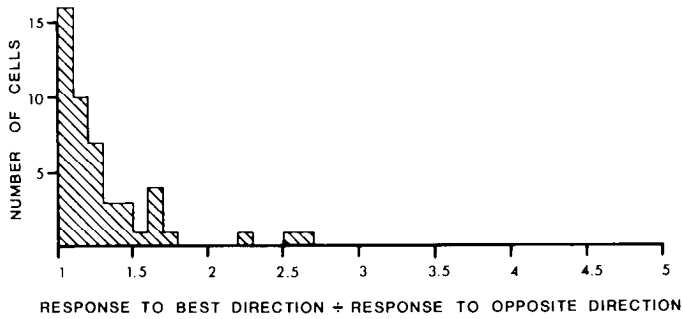


Figure 7. Direction selectivities of 48 cells, measured for each cell as the response to the best direction of an optimally oriented slit divided by the response to the opposite direction. The sample as a whole was quite nonselective, with cells most commonly having a value very close to 1 (identical responses to the two directions).

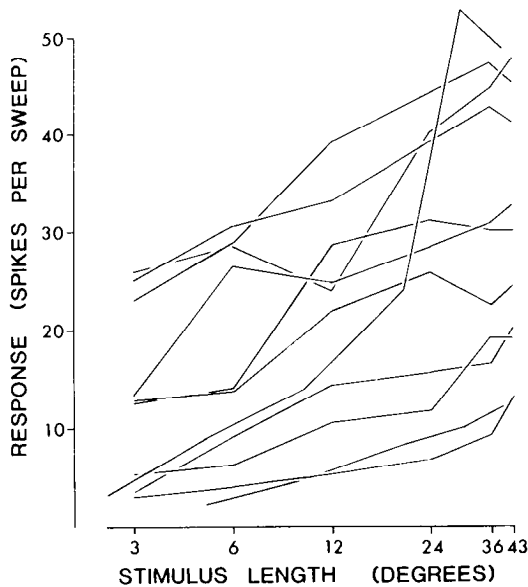


Figure 8. Length-tuning curves for 11 cells. Each point represents the response (defined in the legend to Fig. 1) averaged from 10 or 20 stimulus sweeps. For each cell, six points were obtained, using slit lengths from 3° to 43°. Length is plotted on a logarithmic scale. These curves show the absence of end inhibition among claustral cells and the progressive summation of their responses as the slit was lengthened.

was only a weak correspondence between optimal stimulus length and field location.

The shapes of length summation curves suggested that the central few degrees of the field were more potent than the more distant portions. To test this, we stimulated 2 cells with a slit 43° long that contained a 10° gap. Responses were reduced drastically when the gap was centered in the receptive field, to 57% and 33% of maximum, but increased as the gap was moved away from the center toward one end of the stimulus. When it was 15° away from the receptive field center, responses were as vigorous as to an intact 43° slit. This made it hard to define the limits of most fields because a cell generally did not respond to a slit swept through one end of its field until the slit overlapped a large fraction, sometimes more than half, of the field. The stimulus lengths at which responses reached 75% of maximum thus probably

estimated receptive field lengths more accurately than did the boundaries plotted by hand.

Receptive field borders parallel to the preferred orientation were, in contrast, generally easy to locate, so that this dimension (the width) of the field was measured directly from the hand-plotted receptive field. Some cells had an additional, very weak subfield parallel to the main field and displaced as much as 10° away from it; we could not plot these reliably, but, in response histograms, they produced small peaks distinct from the main response. Whether or not they possessed such subfields, cells did not appear to summate across the widths of their fields, as they responded equally well to wide and narrow light slits or to edges. In Figure 9, receptive field widths are plotted as a function of eccentricity for 193 cells; they showed a slight increase with increasing distance from

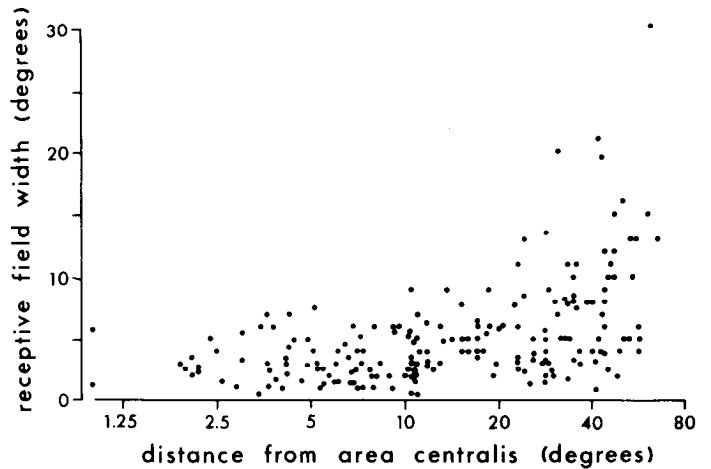


Figure 9. Receptive field width (the dimension perpendicular to the preferred orientation) plotted as a function of receptive field eccentricity for 193 cells. Distance of fields from the area centralis are given on a logarithmic scale.

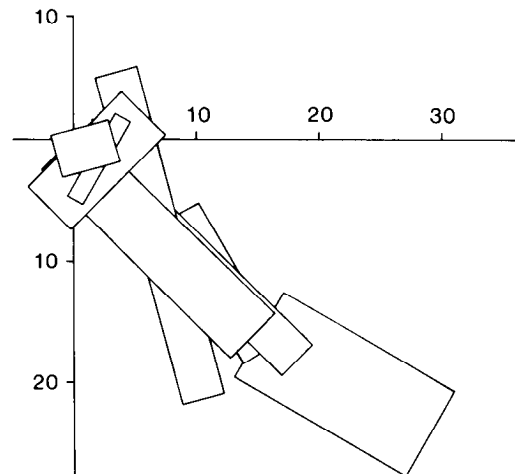


Figure 10. Examples of the sizes and shapes of receptive fields of claustral neurons. These were all plotted along one electrode penetration through the left claustrum. Their lengths (the dimension parallel to preferred orientation) were taken to be equal to the slit length eliciting a response 75% of maximum (see text), while their widths were plotted by hand. Other conventions are as in Figure 5.

the area centralis, but, at any given eccentricity, we found a broad range of widths.

The pronounced length summation, characteristic of cells in the claustrum, resulted from their very long receptive fields. The average ratio of length to width (using the slit length eliciting a 75% of maximum response as a measure of field length) was 6.6:1 ($n = 37$). The actual shapes of some of these fields are illustrated in Figure 10, in which receptive field lengths were taken from length summation curves and the widths are shown as they were plotted by hand.

Moving versus stationary stimuli. For all cells, a moving bar was a far more effective stimulus than a stationary one. Many did not respond at all to a stationary light slit, and only 7 of 29 cells gave a reliable response. Every cell that responded to a stationary slit at its optimal orienta-

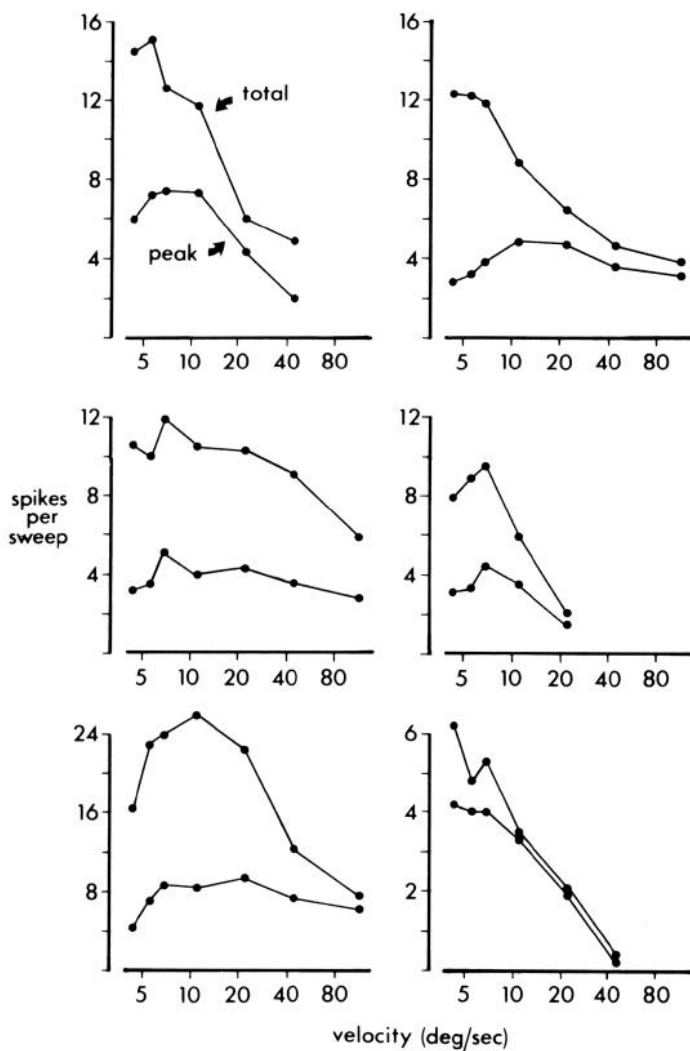


Figure 11. Response plotted as a function of slit velocity for 6 cells. Each point was averaged from 10 to 20 sweeps; stimulus velocity ranged from 4.5° to 112° /sec. Response has been measured in two ways for each cell: as the number of spikes counted over a 1-sec interval, centered on the peak response (labeled *total*), and as the number of spikes counted over a 200-msec interval, at the peak of the response (labeled *peak*). The latter measure yielded the lower curve for all cells and showed less bias toward slow movement.

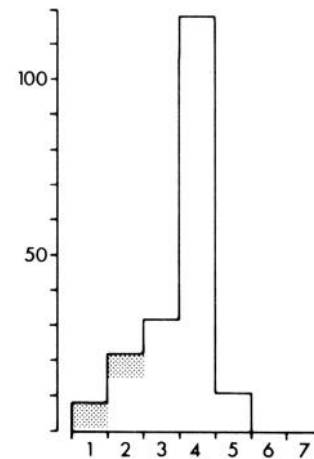


Figure 12. Ocular dominance of 191 cells, classed according to the scheme of Hubel and Wiesel (1962). Cells in *group 1* are driven only by the contralateral eye; those in *group 7* are driven only by the ipsilateral eye; cells in the remaining groups are binocular, with *group 4* cells being those equally influenced by the two eyes. Cells in the *stippled areas* had receptive fields centered in the monocular visual field. Most claustral cells could be driven equally well through either eye.

tion failed to respond to the orthogonal orientation, providing further evidence for orientation selectivity. A few cells seemed to respond only to "on" or only to "off"; because of the weak and erratic nature of these responses, however, we have little confidence in this finding. No cell responded exclusively to light versus dark moving edges nor even showed convincing preferences for one over the other. We could find no evidence of separate "on" and "off" subfields within receptive fields.

So long as a stimulus was moving, its precise velocity did not appear to be very important. We compiled velocity-tuning curves for 21 cells, some of which showed preferences for low velocities, but none showed any sharp selectivity (Fig. 11).

Ocular dominance. Cells in the claustrum were overwhelmingly binocular. Those driven strongly by either eye (*groups 3, 4, and 5* on the ocular dominance scale of Hubel and Wiesel, 1962) outnumbered more monocular cells (*groups 1, 2, 6, and 7*) by a margin of more than 5 to 1 (Fig. 12). Of the cells driven by only one eye, almost all had receptive fields in the monocular visual field, and cells with fields that extended partially into this region accounted for many of those falling in *group 2* (having a strong input from the contralateral eye and a weak one from the ipsilateral eye). Within the binocular region, there was no suggestion of grouping of cells by eye preference.

Discussion

The visual response properties of neurons in the dorso-caudal claustrum resemble those of the visual cortex more closely than do those of any other subcortical region. Like many cells in areas 17, 18, and 19, claustral cells typically require elongated slits or edges, have sharply defined orientation preferences, and summate strongly as the stimulus is lengthened. They lack selectivity for some other stimulus features, such as width, direction of movement, velocity, and contrast (light ver-

sus dark edges), as if they are specialized to deal with only certain aspects of visual information. Because of the response properties of neurons in the claustrum, as well as its limited anatomical connections, we suspect that it performs some rather simple service for the visual cortex that does not require a complex transformation of the information it receives.

An early study of cells recorded at undefined sites throughout the claustrum suggested that they receive convergent input from several sensory modalities (Segundo and Machne, 1956). Subsequent studies have kept alive the notion that polysensory convergence is fundamental to the function of the claustrum (Azzaroni et al., 1968a, b; Spector et al., 1970, 1974), but, in the visual claustrum, we failed to find evidence of responses to other modalities. Although our tests were not particularly thorough, the conclusion that the dorsocaudal claustrum is exclusively visual seems plausible, since the cortical connections of this region are restricted to visual areas (LeVay and Sherk, 1981a). Olson and Graybiel (1980), who have recently mapped the somatosensory, visual, and auditory regions of the claustrum, also noted that cells in these areas responded to only one modality.

Gilbert (1977) and Ferster (1981) have described in some detail the response properties of cells in layer VI of areas 17 and 18, the lamina which provides the visual input to the claustrum. By comparing their findings with those of the present study, we can speculate how the responses of claustral cells are derived from this input.

The two populations are strikingly similar in their length summation. Compared to other cells in areas 17 and 18, those in layer VI summate over remarkably long distances and have correspondingly elongated receptive fields. Their length to width ratios average 4.8:1 in area 17 and 4.9:1 in area 18 (Gilbert, 1977; Ferster, 1981), not much less than the average in the claustrum, which was 6.6:1. The absolute lengths of receptive fields in layer VI were, on the whole, shorter than in the claustrum: the median length in area 17 was 8° (Gilbert, 1977) and, in area 18, 6° (Ferster, 1981), while, in the claustrum, the median 75% point of length-tuning curves was 12.5° .

A second major similarity between the two populations is their orientation selectivity. The median half-width at half-height of the orientation-tuning curves of the claustral cells in the present study was 27° . Published studies of orientation tuning in the cortex, which have pooled data from all layers, have reported median values ranging from 11.5° to 29° with an average of 20° (Campbell et al., 1968; Henry et al., 1974; Rose and Blakemore, 1974; Watkins and Berkley, 1974; Ikeda and Wright, 1975; Sherk and Stryker, 1976; Nelson et al., 1977; Hammond and Andrews, 1978; Heggelund and Albus, 1978; Kato et al., 1978; Leventhal and Hirsch, 1978; Murphy and Berman, 1979). According to Gilbert (1977), neurons in layer VI are generally about as sharply tuned as the overall cortical population. These findings suggest that claustral cells are somewhat less selective for orientation than are cells in cortical layer VI. Even so, if several cortical cells converge on one claustral cell, their preferred orientations must be rather well matched. Particularly if these cells lie in different cortical areas, the convergence of

their axon terminals onto a common target population must present a formidable matching problem. The existence of orientation domains in the claustrum simplifies this problem substantially, since the match between afferent and recipient becomes a match between regions rather than between individual neurons.

Because of their poor responses to stationary stimuli, it was necessary to test the orientation tuning of most claustral cells using moving stimuli. This raises the question of whether the selectivity of their responses represented a true orientation specificity or, instead, a selectivity for an axis of motion. We were unable to determine whether claustral neurons preferred a particular axis of movement when tested with a stimulus lacking an oriented edge, i.e., a small spot, since they did not respond to such stimuli. However, this very requirement for long slits or edges can be taken as evidence of orientation selectivity. The fact that the slit had to be oriented correctly may well have derived from the summation that these cells showed along the long axis of their receptive fields, coupled with their lack of summation in the orthogonal direction. Whether other mechanisms also play a role in generating orientation selectivity in the claustrum remains to be investigated.

In addition to the resemblances between the layer VI cells of areas 17 and 18 and cells in the claustrum, there are two notable differences. First, layer VI cells tend to be dominated strongly by one eye (Gilbert, 1977; Harvey, 1978; Ferster, 1981), while claustral cells are binocular. Only about 40% of the cortical populations respond well through either eye (falling in ocular dominance groups 3, 4, or 5 of Hubel and Wiesel, 1962) compared to 84% of our claustral sample. Second, layer VI cells are, on the whole, the most direction selective in the cortex; 50% of those in area 17 and 85% of those in area 18 in Gilbert's and Ferster's samples responded at least 10 times as well to one direction of motion as to the other, a level of selectivity greater than anything seen in the claustrum. The generation of binocular, bidirectional responses from monocular, strongly direction-selective inputs could be explained by convergence of cortical afferents, though it seems somewhat odd to generate these selective characteristics at one level and then throw them away by pooling inputs to the next. Not all cells in layer VI are so selective, however. Given that only 3 or 4% of the cells in layer VI project to the claustrum (LeVay and Sherk, 1981a), it is possible that the input to the claustrum originates from the small fraction of cells in this layer that are binocular and nondirectional. These might also be the cells showing the greatest degree of length summation. It would be of interest to study the properties of this subpopulation directly to determine whether they differ from those of the separate and much larger population of layer VI cells that project to the lateral geniculate nucleus (Gilbert, 1977; Harvey, 1978).

Several other visual cortical areas also project to the claustrum and thus doubtless contribute to the response properties of claustral neurons. No laminar analyses of these other areas have been performed, but a striking property of the posteromedial lateral suprasylvian area (PMLS), for example, is the predominance of unidirec-

tional responses (Hubel and Wiesel, 1969; Spear and Baumann, 1975). Again, this is in contrast to what is found in the claustrum.

The most pressing question raised in this investigation of the visual claustrum is that of its effect on visual cortex. Although cortical and claustral cells share certain response properties, in other respects, they contrast sharply, and these differences place some limits on hypotheses that one might make about the role of the claustrum in cortical visual processing. First, the elongated visual fields of claustral cells and their consequent requirement for very long stimuli distinguish them from all cortical cells but those in layer VI. Outside of this layer, in fact, receptive fields can hardly be called elongated, since their average length to width ratio (in area 17) is only 1.2:1 (Gilbert, 1977). Second, as a corollary of their remarkable length summation, claustral receptive fields are virtually free of end inhibition. Yet, in the cortex, this property is common and is potent enough in about one-third of all area 17 cells to reduce responses by half (Ferster, 1981; Gilbert, 1977; Kato et al., 1978; Rose, 1974). A third difference involves direction selectivity. About 75% of the cells in area 17 respond at least twice as well to one direction of movement as to the other (Gilbert, 1977; Kato et al., 1978; Murphy and Berman, 1979; Singer et al., 1975), while only 3 of 48 cells in the claustrum reached this criterion level. Lastly, claustral cells as a group are much more binocular than those in visual cortex. The contrast in response properties between the claustrum and the cortex becomes even more striking if one considers only the properties of neurons in layer IV, the lamina that receives the heaviest innervation from the claustrum.

These differences in response properties make claustral cells unlikely candidates to provide the primary driving input to any substantial fraction of cortical cells. The more numerous axons from the lateral geniculate nucleus, together with the axon collaterals of cells in layer VI (Gilbert and Wiesel, 1979), undoubtedly form the dominant input to layer IV. It may be possible to clarify the contribution made by the claustrum to receptive field properties in layer IV by inactivating the nucleus and examining the consequent changes in cortical response properties.

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