Phase-shifted EOD's are coded differently from normal ones (Fig. 2, E and F). As ϕ approaches 90°, the threshold for 1:1 firing increases, jitter in spike latency increases, the latency difference between one polarity and the reverse decreases slightly, and the difference in threshold for 1:1 firing for the two polarities decreases. Time-reversed EOD's evoked spikes differing in latency by only 0.1 msec (Fig. 2, G and H). Any or all of these changes may render phase-shifted EOD's less effective during playback experiments.

We tested the behavioral significance of the 0.4-msec difference in spike latency in one additional playback experiment by presenting a solitary male with rectangular waves (*14*) of variable duration (Fig. 1E). At the receptor level, rectangles evoked a single spike on the leading edge when outside became positive; inversion of the polarity shifted the spike to the trailing edge. All stimuli were driven by the scrambled female SPI. This male produced rasps for rectangular waves of 0.4 msec but not for 0.1 msec nor for 1.6 msec. For this paradigm, he failed to discriminate an 0.4-msec rectangle from a female's EOD. We conclude that species recognition depends on a two-spike code evoked by the species-specific EOD. Additional studies indicate that EOD's of sympatric species do not elicit rasps, nor do they evoke the same neural code from *Knollenorgans* (*11*).

To have species recognition rely upon a simple code comprising only two spikes separated by the appropriate interval may be unique for electric communication, where the channel is exploited by fewer users than auditory channels. Temporal coding may be especially advantageous for the electric modality, where signal waveforms are invariant because signal conduction is instantaneous and there are no echoes. Temporal cues are also regarded as important in recognition of auditory signals, especially in invertebrates (*15*).

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6. The preserved specimens were identified as *Brienomyrus brachyistius* by L. Taverne at the Musée Royal de l' Afrique Centrale, Tervuren, Belgium, but we later distinguished four morphologically similar species on the basis of discrete differences in EOD's. The temporary name, *triphasic*, refers to the three-phase waveform of the EOD typical of both males and females.
7. Sex differences in the EOD's of electric fish were first discovered in the quasi-sinusoidal (wave) discharge of *Sternopygus macrurus*. [C. D. Hopkins, *Science* **176**, 1035 (1972)].
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9. Mormyrids have three receptor types for electroreception—*Knollenorgans*, mormyromasts, and ampullary receptors. *Knollenorgans* function solely in communication. They are adapted to receiving weak electric signals from other fish; they are the most sensitive class of tuberous receptors; and the responses are always phase-locked to the pulse stimulus, thereby preserving temporal information. Most important, *Knollenorgan* afferents project to the nucleus of the lateral line lobe, where interaction with a corollary discharge from the electric organ pacemaker inhibits signals to the mesencephalon [B. Zipser and M. V. L. Bennett, *J. Neurophysiol.* **39**, 713 (1976)]. Thus, the fish never "hears" its own EOD on its *Knollenorgan* system, hence its putative role in communication.
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13. The fish was gently restrained with smooth Plexiglas rods. We played EOD-like stimuli to 30 *Knollenorgans* in six *B. brachyistius triphasic* and found no response variation over the body surface.
14. The power spectrum of a rectangle wave differs from that of the female's EOD.
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16. We thank the French CNRS [Centre National de la Récherche Scientifique (France)] for generous support during our visit to the field station in Makokou, Gabon, and G. Michaloud and S. Michaloud for local logistic help. R. Lewis helped with the fieldwork, V. M. Wong drew the fish, J. Bastian and N. Viemeister helped improve the manuscript, and C. Knox thought of time-reversing the EOD. Supported by NIMH grant MH26140, NIH postdoctoral program NS06309, the National Science Foundation, the National Geographic Society, and the Graduate School of the University of Minnesota.

15 August 1980; revised 14 November 1980

Visual Claustrum: Topography and Receptive Field Properties in the Cat

Abstract. *A region containing visually responsive cells was found in the dorsocaudal claustrum. This area contains a single orderly map of the contralateral visual field. Like cortical cells, most claustral cells are selective for stimulus orientation. They are binocular, and they respond to either direction of movement and to a broad range of velocities. Their most striking property is a marked preference for very long stimuli.*

The claustrum is a narrow strip of gray matter in the forebrain of mammals, sandwiched between the putamen and the insular cortex. It is reciprocally connected with the entire neocortex, the corticoclaustral projection arising from pyramidal cells in cortical layer VI and the return pathway terminating most densely in layer IV (*1*). In the cat, a visually responsive region at the caudal end of the claustrum has been described by the use of evoked potentials (*2*). We have studied the organization of this region using standard single-unit recording techniques (*3*), with the hope of casting light on the function of the corticoclaustral loop.

Tungsten electrodes were used to record from the claustral visual area in 13 cats anesthetized with pentobarbital and paralyzed with gallamine. For the mapping of the visual field representation in the claustrum we have relied principally on results from four cats in which 43 vertical electrode penetrations were made through the visually responsive area. In the remaining animals, recordings were made primarily for the purpose of studying receptive field properties or injecting neuroanatomical tracers, but in addition these experiments provided confirmation of the mapping results.

In coronal sections (Fig. 1A, inset) the claustrum is comma-shaped, with an expanded dorsal region and a narrower, laterally curving stem. At the anterior limit of the visual region (about 4.0 mm in front of the caudal tip of the claustrum) the dorsal surface is flat and slanting, while farther back it becomes narrower and rounded. On a typical vertical electrode penetration, the cells first encountered at the dorsal surface of the claustrum had receptive fields in the far periphery of the contralateral visual field; as the electrode was advanced, receptive fields moved rapidly toward the vertical meridian, sometimes even crossing it and ending centered as much as 10° into the ipsilateral visual hemifield. In general this movement of fields toward the vertical meridian was accompanied by an upward drift in field positions. On such a traverse, virtually all cells were responsive to visual stimulation and none to tactile or auditory stimuli. Cells below this region, which might be 0.5 to 2.0 mm thick depending on the anteroposterior level, were unresponsive to visual stimuli, indicating that the visual area occupies only the dorsal portion of the caudal claustrum (*4*).

Penetrations through the caudal tip of the claustrum yielded progressions of receptive fields across the upper part of the visual field; those in the middle of the visual region gave progressions roughly along the horizontal meridian, and those through the anterior part of the visual region resulted in receptive field movements across the lower half of the visual field (Fig. 1A). In contrast, when penetrations were made at different mediolateral positions in the same coronal plane, the progressions of receptive fields resembled each other, although receptive fields tended to be somewhat higher on more lateral penetrations. On penetrations close to the medial edge of the claustrum (and on those close to the lateral edge at posterior levels), receptive fields moved in toward the vertical meridian and then moved out again toward the periphery.

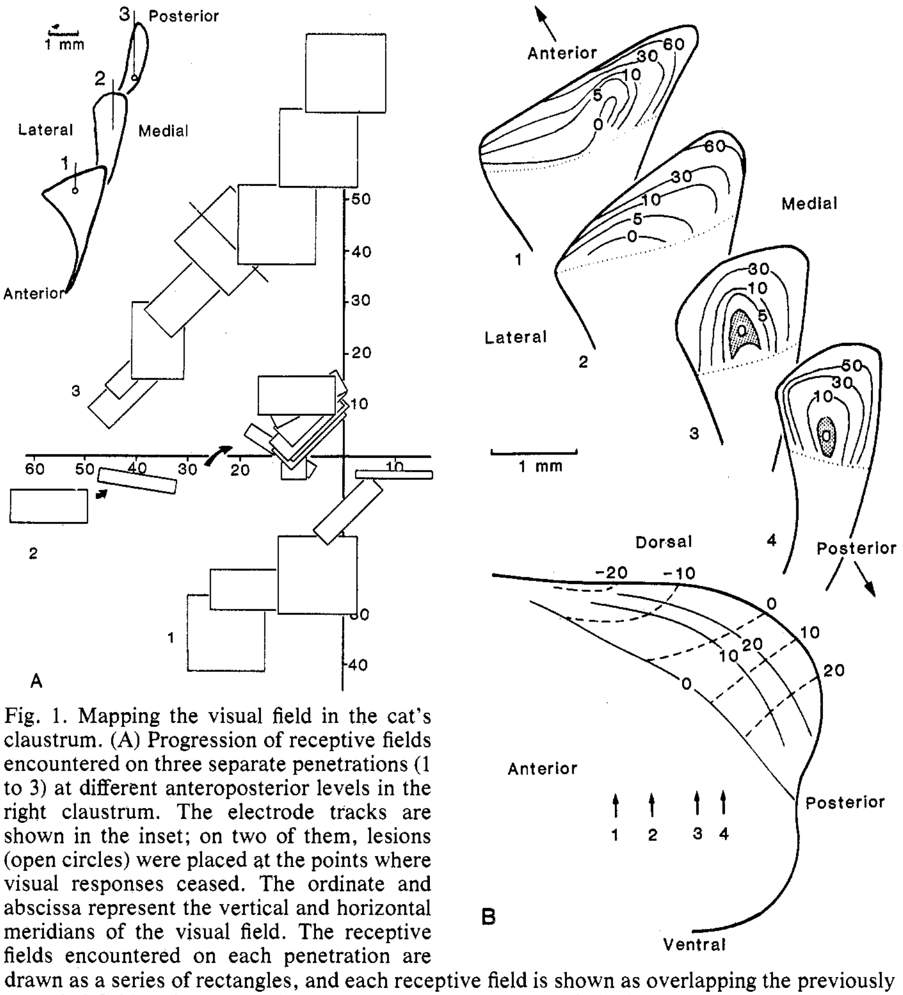

Fig. 1. Mapping the visual field in the cat's claustrum. (A) Progression of receptive fields encountered on three separate penetrations (1 to 3) at different anteroposterior levels in the right claustrum. The electrode tracks are shown in the inset; on two of them, lesions (open circles) were placed at the points where visual responses ceased. The ordinate and abscissa represent the vertical and horizontal meridians of the visual field. The receptive fields encountered on each penetration are drawn as a series of rectangles, and each receptive field is shown as overlapping the previously recorded field. Where they do not overlap the progression is indicated by arrows. Receptive fields were plotted about every 100 μm (penetrations 1 and 2) or 200 μm (penetration 3). The length of each receptive field (parallel to the preferred orientation) has been arbitrarily drawn as 15°, although most were in fact longer. Widths are shown as they were plotted with optimally oriented light slits. Fields of cells without orientation preference are represented by 15° squares. Preferred orientations are indicated by the long axes of the fields, or in a few cases by a line bisecting the receptive field. Almost all receptive fields are in the left (contralateral) half of the visual field. The three penetrations all yielded progressions of receptive fields from the periphery toward the vertical meridian, but at different elevations: on penetration 1 (most anterior), fields were in the lower part of the visual field; on penetration 2, they were near the horizontal meridian; and on penetration 3 (most posterior), they were in the upper half of the visual field. (B) Reconstruction of visual field map. Upper part is a series of coronal sections. The lower limit of the visual area is shown by a dotted line and the vertical meridian by shaded areas (in the two most posterior sections). Solid lines indicate distances from the vertical meridian, with the far periphery being represented most dorsally; elevations are not shown. The lower drawing is a section taken lengthwise through the claustrum. Note that the visual area is restricted to its dorsocaudal part. The solid lines show isoazimuths, and the dashed lines show isoelevations.

A map of the visual field representation, in four coronal sections and in a longitudinal section cut along the rostrocaudal axis of the claustrum, is shown in Fig. 1B. The entire contralateral half of the visual field is represented, with the far periphery at the dorsal surface of the claustrum, and the vertical meridian at the lower border of the visual region. Upper fields lie caudally and lower fields rostrally, with each elevation being represented by a plane tilted back from the coronal plane. Because the two-dimensional visual field is here mapped onto a three-dimensional structure, single visual field points are represented as lines. Caudally these projection lines are strongly curved, matching the curvature of the claustral surface and enwrapping the vertical meridian representation on three sides. Rostrally this pattern becomes flattened to conform to the flattening of the claustral surface, and the projection lines are bent downward only at the medial edge of the nucleus. From this map we have formed the distinct impression that the peripheral part of the field is overrepresented in comparison with its representation in the primary visual cortex (area 17). The deformation of the claustral map, as compared with cortical maps, may be related to the claustrum's lack of lamination, which in cortex restricts distortions in the third dimension.

The general layout of the visual field map in the claustrum was confirmed anatomically: [^{3}H]proline was injected in area 17 at sites representing visual field points located by recording through the injection pipette, and the resulting projection zones in the claustrum were charted by autoradiography. Each zone was elongated mediolaterally, its orientation and curvature matching the line found physiologically to represent the corresponding visual field point. In addition, [^{3}H]proline injections at defined sites in areas 18, 19, and the largest of the lateral suprasylvian visual areas [area PMLS (*5*)] indicated that four visual field representations in the ipsilateral cortex project retinotopically onto a single claustral map.

Because of the substantial input from the visual cortex to the claustrum, we compared the receptive field properties of claustral cells with those of visual cortical neurons. Like cortical cells, most claustral cells responded best to appropriately oriented moving bars or edges. They also resembled cortical cells in having little spontaneous activity. Responses to stationary stimuli were often very poor, but whenever present, such responses could only be elicited by properly oriented elongated stimuli, confirming that cells were indeed orientation-selective. For the quantitative study of receptive field properties, response histograms were obtained through the use of a variety of slit orientations, lengths, and velocities.

From these data, orientation tuning curves were constructed for 54 cells, four examples of which are shown in Fig. 2A. Half-widths at half height (the amount a stimulus must be rotated away from the optimal orientation to reduce the response by half) ranged from 6° to 56°. The mean value of 28° was somewhat broader than the value reported for cells in area 17 (*6*). Only 3 percent of the total population studied lacked a preferred orientation, indicating that this is a significant stimulus variable for the visual claustrum. We frequently observed sequences of similar or gradually changing preferred orientations during vertical penetrations, just as are found in area 17 (*3*); on penetration 2 of Fig. 1, for example, preferred orientations rotated clockwise through 180°. The layout of these regions of common orientation preference within the claustrum remains to be investigated.

The most striking property of claustral units was their requirement for very long stimuli. The responses of 48 neurons were studied quantitatively as a function of slit length (Fig. 2B). Many cells responded increasingly well as the slit was lengthened to 43°, our longest available stimulus, and, on the average, a 16° slit was required to elicit a 3/4-maximal response. Short slits (2.5° or 5°) usually elicited only feeble responses, even when swept over the central part of the elongated field; even so, stimulation of this central region was important to the cell's response, since long stimuli that did not include this region elicited a weak response or none. The receptive field organization of claustral cells is remarkably similar to that described by Gilbert (*7*) for a population of neurons in layer VI of area 17, the layer that gives rise to the corticoclaustral projection.

In other respects claustral cells tolerated variation of the stimulus. Most cells (118 of 191) responded equally well to stimulation of either eye. None were strongly dominated by the ipsilateral eye, and of those strongly dominated by the contralateral eye, most had receptive fields in or near the monocular segment of the visual field. Almost all cells responded equally well to either direction of stimulus movement and equally well to light or dark bars. In general, they were broadly tuned for velocity; those that showed any selectivity preferred slow movement.

Since their receptive fields are longer than any reported in area 17, it seems likely that claustral cells receive a convergent input from neurons having similar preferred orientations located over a considerable extent of cortical territory. Such convergence may well account for the lack of selectivity for direction of movement and for the lack of strong eye preference.

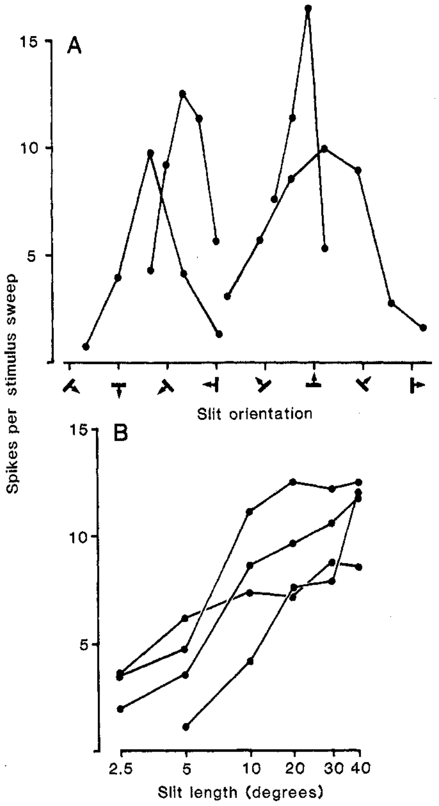

Fig. 2(A). Orientation tuning curves for four claustral cells. Each point is the averaged response to ten stimulus sweeps. A range of orientations centered around the optimal orientation was tested for each cell, through the use of a 40° by 0.75° light slit viewed by the contralateral eye. Only one direction of movement was used for each orientation. Although not shown, both directions of movement at the optimal orientation elicited similar responses. (B) Stimulus length tuning curves for the same four cells as in (A). The stimulus was a 0.75° bar at the optimal orientation. These cells were typical in showing a marked preference for very long stimuli.

Many cells in layer VI of the visual cortex project to the lateral geniculate nucleus (LGN) (*8*). We have shown by a double-label retrograde transport experiment that the cells projecting to the claustrum form a separate population from those projecting to the LGN (*9*). Whether the two populations are functionally distinct remains to be investigated. Another problem, as yet unapproached, is how the claustral output back to the visual cortex contributes to the response properties of neurons there.

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9. Horseradish peroxidase (HRP) was injected into the claustrum, and D-[^{3}H]aspartic acid [P. Streit, E. V. A. Knecht, M. Cuenod, *Science* **205**, 306 (1979); R. W. Baughman and C. D. Gilbert, *Nature (London)* **287**, 848 (1980)] was injected into the LGN. Sections of area 17 prepared for both HRP histochemistry and autoradiography showed many cells in layer VI labeled with either HRP reaction product or overlying silver grains, but none with both labels. That cells projecting to the claustrum can transport D-aspartic acid was shown by a control injection of D-[^{3}H]aspartic acid into the claustrum, which also produced labeling of layer VI cells in area 17.
10. We thank R. Leibowitz for histological assistance and U. Dräger, C. D. Gilbert, and R. Masland for comments on the manuscript. This work was supported by grants EYR01-1960 and IF 32 EY 05269 from the National Institutes of Health. S.L. is the recipient of research career development award EY 00090.

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