Receptive-Field Transformations Between LGN Neurons and S-Cells of Cat Striate Cortex

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SUMMARY AND CONCLUSIONS

1. To determine the functional transformation in the processing step between lateral geniculate nucleus (LGN) and striate cortex, the receptive-field characteristics of 50 directly driven, lamina 4 S-cells were compared with those of a similar number of LGN neurons. Experiments were performed on paralyzed and anesthetized adult cats.

2. A signature was established for the responses of LGN neurons by observing the responses to thin light and dark moving bars and, after allowing for latency, by comparing these responses with the flashing-bar receptive field. Evidence of this signature was then sought in the responses of S-cells to similar stimuli.

3. When stimulated with moving bars, on-center LGN neurons responded with a strong discharge to a light bar followed, in spatial position, by a discharge to a dark bar. When compared to the flashing-bar receptive field, the light-bar discharge corresponded with the near side of the receptive-field center and the dark-bar discharge with the far side. Off-center LGN neurons generally gave a complementary pattern to the one above. Brisk sustained (BS) and brisk transient (BT) LGN units showed similar results.

4. By identifying the signature of LGN neurons in the responses of S-cells it was possible to recognize at least two and possibly three arrangements in the inputs to these cells. Individual S-cell responses could be explained as arising from: a) a single type (on- or off-center) of LGN neuron, b) two types (on- and off-center) of LGN neurons with their receptive fields placed side by side along the line orthogonal to the optimal orientation, c) three types of LGN neuron. Only a small number of S-cells were placed in the c category. There is doubt about the existence of the tripartite input, since in certain respects the responses of these cells resembled those of cells receiving a single or dual input. In all three groups, S-cells were found receiving inputs from either the fast (BT) or slow (BS) stream.

5. In the population of dual-input S-cells, the separation between the centers of on- and off-responses distributed over a range similar to that found for the diameters of the receptive-field centers in parent LGN neurons. This was the case for cells in either the fast (BT) or slow (BS) streams.

6. Along the line parallel to the optimal orientation the receptive-field length of S-cells, measured by the method of length summation, ranged over a distance twice that of the receptive-field center diameters in the parent LGN neurons.

7. An estimate was made of the number of LGN neurons contributing to the receptive fields of single S-cells in lamina 4. After making certain assumptions about the distributions of inputs to the S-cell receptive field, it was estimated that the response in each discharge region came from 1 to 20 like LGN neurons. It is argued that the receptive-field midpoints of these afferents are scattered over a circular area, whose diameter is equal to the receptive-field center diameter of one of the afferent LGN neurons (0.4° for BS and 0.8° for BT neurons).

INTRODUCTION

It is now almost 20 years since Hubel and Wiesel (22) placed the simple cell (substantially equivalent to the S-cell of our termi-
nology (17)) at the first of the processing stages in cat striate cortex. Subsequent studies, in which response latency was measured after electrical stimulation in the optic radiations (20, 40, 43), have confirmed the primary position of the S-cell.

It is appropriate, therefore, in investigating the LGN-cortex transformation to study the differences in the receptive fields of LGN neurons and S-cells. From investigations on the response patterns of concentric receptive fields of retinal ganglion cells (and LGN neurons) (33, 34) a unique signature can be derived for on- and off-center geniculate inputs. To fulfill this aim, we have applied the same methods for assessing the afferent supply to striate neurons we progressed to the present comparison of quantitatively recorded properties of the two types of LGN neurons (BS and BT) and each of two groups of monosynaptic S-cell in lamina 4 and in lamina 6. The results of this study are subdivided so that in this paper we concentrate on the receptive-field transformation in going from LGN neurons to monosynaptic S-cells in lamina 4, while in the accompanying paper (29) attention is directed toward the receptive-field differences among the two types of first-order S-cell in lamina 4 and those in lamina 6.

METHODS

Preparation

A detailed description of the methods has been published elsewhere (6, 20) and only a brief outline is given here. Adult cats were initially anesthetized with halothane and canulas were inserted in the trachea and the cephalic vein. Bilateral cervical sympathectomy was performed to reduce the eye movements (32). After injecting the wounds with long-lasting local anesthetic (Marcaine) the animals were paralyzed and artificially respiried with a mixture of nitrous oxide and oxygen (70/30). The level of ventilation was adjusted to keep the percentage of CO$_2$ in the expired gases at 4-4.5%. Paralysis was achieved by the infusion of gallamine triethiodide (Flaxedil), 16 mg·kg$^{-1}$·h$^{-1}$ and $d$-tubocurarine chloride (Tubarine), 1.6 mg·kg$^{-1}$·h$^{-1}$ in a solution of plasma-lyte 148 (Travenol) to which a small quantity of pentobarbital sodium (Nembutal), 1.2 mg·kg$^{-1}$·h$^{-1}$ was added.

The corneas were covered with plastic contact lenses with no optical power and correcting lenses, determined by retinoscopy, were added to focus the eyes at 1 m. Artificial pupils (3-mm diameter) were centered on the visual axis with the aid of an indirect ophthalmoscope. Single units were isolated either with tungsten-in-glass (27) or glass-coated platinum-iridium (47) microelectrodes. A small dural opening was made for the insertion of the tungsten-in-glass microelectrodes, whereas the glass-coated platinum-iridium microelectrodes were pushed through the dura mater. The properties of each unit were qualitatively assessed by using moving and flashing bars or spots of light of variable size and a variety of black targets. Neurons in the cortex and the lateral geniculate nucleus were classed according to criteria described previously (11, 17, 20). The receptive fields of all these units were situated within 12° of the midpoint of the area centralis.

Electrical stimulation

Cortical neurons receiving a monosynaptic input from the thalamus were identified by a method of electrical stimulation involving the use of one pair of bipolar stimulating electrodes in the optic chiasm (OX) and two pairs in the optic radiations (OR). A full account of this method has been published previously (6). Briefly, cortical units were classed as monosynaptic if they were driven from both pairs of stimulating electrodes in the optic radiations and if the orthodromic latency to stimulation at the site closest to the cortex (OR$_1$) was equal to or less than 1.6 ms. Lateral geniculate axons isolated in the cortex were recognized from their short and unchanging latencies to electrical stimulation and also from their aptitude to follow high frequencies (150 Hz) of repetitive
stimulation. Difference in the signal conduction time from the stimulating electrode, OX, in optic chiasm to the one low in the optic radiations just above the LGN (OR,) provided the information to determine if the afferent stream to the cell was fast or slowly conducting (7).

**Histological methods**

The laminar position of cells recorded in the cortex was determined by making small electrolytic lesions (5 µA for 5 s) every millimeter along the electrode track. At the end of the experiment, the animal was deeply anesthetized with Nembutal and perfused through the heart with 10% neutral-buffered Formol saline. Frozen sections (40 µm) were prepared and stained with neutral red. The electrode tracks were reconstructed and each neuron was positioned along the track according to its separation, recorded during the experiment, from the nearest lesion.

**Quantitative examination of receptive fields**

A cathode-ray oscilloscope (Hewlett-Packard 1321A) under computer control was used for the generation of visual stimuli for the quantitative assessment of the response patterns of recorded neurons. A raster, created with a time base of 100 Hz (10 ms/sweep) and a scan of 50 kHz (10 µs/line) in the cathode-ray oscilloscope (CRO), produced an image of a 1,000 parallel lines across the screen. Each one of these lines could be resolved electronically into 256 divisions. Light and dark bars were constructed under computer control by intensifying or dimming at selected times during the 10 ms required to trace the raster. The area of screen covered by the raster could be varied but was set to be either 9 x 9° or 18 x 18°. Within this 9 x 9° area the smallest possible bar was 0.5′ arc wide x 2.0′ arc long. Changes in bar orientation were achieved by rotating the raster, while movement of the bars came by displacing the points of intensifying or dimming to a new line with each generation of the raster (every 10 ms). Movements at high velocities (>25°/s) proved unsatisfactory because of the large image displacement from one raster generation to the next. Hand-held stimuli, matched for velocity with stimulus moving on the CRO, were used to assess cutoff velocities in these instances. The luminance of the background produced by the tracing of the raster was 0.34 cd/m², while that for the light bar ranged from 1.72 to 2.72 cd/m², and that for the dark bar from 0.03 to 0.11 cd/m². In the experiments with flashing bars the switch-on time simply depended on the time the beam took to generate the image (about 10 ms), while the switch-off time was related to the persistence of the P4 white phosphor (60 µs to 10%). Recording of the flashing light response generally occurred over a duration of 800 ms after light on or off: to avoid a response overflow into the next stimulus phase, the stimulus was held without changing for periods as long as 2 or 3 s.

It was possible to change a selected feature of the stimulus at the end of each stimulus cycle, and in this way to build up a multihistogram for a range of values in this feature (19). Both the dimensions of the stimulus itself and the extent and starting point of its sweep could be modified for this purpose. All histograms were stored for further analysis on magnetic tape.

**RESULTS**

In the presentation of the results we set out to follow the transformation of receptive-field properties between neurons of the lateral geniculate nucleus and their recipient S-cells in the striate cortex. There are, therefore, two populations of cells involved in this study: the first comprises relay cells in the laminated LGN and the second, the S-cells of laminae 4 in the striate cortex.

**Response patterns of LGN neurons to light and dark bars**

Quantitative analysis was carried out on the response properties of 59 LGN units, which comprised 22 axons and 37 neurons. The axons were isolated during electrode penetrations of the striate cortex and were identified from their responses to electrical stimulation (6, 20). The neurons were recorded in those parts of the LGN with a retinotopic position similar to that found in the sample of striate neurons. The receptive fields of 50 units lay within 8° of the midpoint of the area centralis and only 9 units were more peripherally situated at eccentricities between 8 and 12°.

**RESPONSE PATTERNS.** Typical response patterns of an on-center LGN unit to light and dark bars are represented in the average response histograms of Fig. 1. In Fig. 1A the thin line histogram shows the response to a light bar (0.1° wide x 1.2° long) moved across the receptive field, and the thick line histogram, the response to a dark bar moved in the same direction. The thin and thick line convention for representing light and dark bar responses is maintained throughout this paper. All the stimulus parameters were identical for both light and dark bars so that the histograms could be compared on the same time axis. In Fig. 1B the pair of his-
BULLIER, MUSTARI, AND HENRY

FIG. 1. A: response pattern given by an on-center BS neuron in the LGN to light (thin line) and dark (thick line) bars for one direction of movement. B: response pattern of the same unit for bar movement in the opposite direction. Note time axis increases from left to right in both A and B. C: histograms in B are flipped over and positioned beneath those of A so that in each dimension a point on the axis corresponds to the same position in the stimulus sweep (see text). Note that no account has been taken of the cell’s response latency to moving stimuli. A, B, C: moving bars 0.1 x 1.2°, 20 sweeps at 1.83°/s.

A

B

C

0 1.6 3.2
Time (sec)

70
Sp/sec

0.5°

QC 21.1.3

1A and B were combined so that a point on the common X axis corresponded to a given position in space. This step is shown in Fig. 1C where the histograms of Fig. 1B are flipped over and positioned underneath the histograms of Fig. 1A. The resulting combination provides a representation of the response of the cell for common positions of the bar as it moves along the initial or reverse direction.

This mode of presentation is used in Fig. 2 to display the response patterns to light and dark bars for six on-center LGN units. From the histograms of Fig. 2 it is apparent that all six units had a central region of strong response to a light bar. Since no allowance was made for any delay due to response latency, these response peaks showed variable amounts of relative displacement (latency adjustments have been made in the histograms in Fig. 5 and subsequent figures). On the far side of the central region producing the light-bar discharge, there was a region of dark-bar discharge; this varied from a strong response (Fig. 2A and D), to more commonly a weak response (Fig. 2B and E), and sometimes to no response (Fig. 2C and F). In addition, there was occasionally a region of light-bar discharge beyond the region of dark-bar discharge. This is most obvious in Fig. 2A, where three discharge peaks can be seen for each direction of movement; the first is the central component response to a light bar, then comes the response to a dark bar, and finally the secondary response to a light bar.

Similar response patterns to those of Fig. 2 have been found for both types of LGN units (brisk sustained and brisk transient), providing the major input to lamina 4 (8, 16). Thus Fig. 2A, B, and C show the response patterns of on-center BS units and Fig. 2D, E, and F of on-center BT units. Generally the response patterns to moving stimuli were the same for these two cell classes.

For comparison, the response patterns of off-center LGN units to light and dark bars are presented in Fig. 3. These patterns are the complement of those for the on-center unit. Thus, in the discharge for each direction of movement there is a central region of dark-bar discharge, followed by a light-bar discharge, and occasionally a second
FIG. 2. Response patterns given by on-center neurons in the LGN to light and dark moving bars. Same convention as in Fig. 1. A, B, C: brisk sustained (BS) units; D, E, F: brisk transient (BT) units. Bar sizes and velocities (close to optimal): A: 0.1 x 0.7” moving bars, 20 sweeps at 0.92/s. B: 0.15 x 0.7” moving bars, 20 sweeps at 1.83/s. C: 0.1 x 0.5” moving bars, 20 sweeps at 0.92/s. D: 0.1 x 0.7” moving bars, 20 sweeps at 0.92/s. E: 0.1 x 2.9” moving bars, 40 sweeps at 1.83/s. F: 0.1 x 1.23” moving bars, 20 sweeps at 7.32/s.

dark-bar discharge, as in Fig. 3F. Unlike the pattern for on-center units, that nearly always showed a strong central response to a light bar, a number of off-center units gave only a weak response to a dark bar, which was often even weaker than the light-bar response (see Fig. 3C and F). Like on-center cells, there was no noticeable difference be-
FIG. 3. Response patterns given by off-center LGN units to light and dark moving bars. Same conventions as in Fig. 1. A, B, C: brisk sustained (BS) units; D, E, F: brisk transient (BT) units. Bar sizes and velocities: A: 0.1 x 0.7° moving bars, 20 sweeps at 0.92°/s. B: 0.1 x 0.7° moving bars, 40 sweeps at 0.92°/s. C: 0.1 x 0.5° moving bars, 20 sweeps at 0.92°/s. D: 0.1 x 0.6° moving bars, 20 sweeps at 0.92°/s. E: 0.15 x 3° moving bars, 80 (dark bar) and 40 (light bar) sweeps at 3.66°/s. F: 0.2 x 1.1° moving bars, 20 sweeps at 1.83°/s.

Between the patterns for BS (Fig. 3A, B, and C) and BT units with off-centers (Fig. 3D, E, and F).

Population variability in response patterns. The variability found in the response patterns of LGN neurons makes it
difficult to link moving-bar responses in striate and LGN neurons. In the patterns in Figs. 2 and 3 we have attempted to show the extent of this variability so that a range of expectations can be drawn up for striate neurons. It is apparent from these figures that the response to a light or dark bar in either direction may produce only a single central response component or, alternatively, there may be two, or the full complement, of three discharge peaks.

In spite of the restrictions that variability in the discharge patterns of LGN neurons impose on any attempt to anticipate the response of striate neurons, there is one feature that seems common to the responses of the majority of the LGN population. Thus, with the exception of some peripheral units with large receptive fields, there is an obvious discharge from the central region of the receptive field when a bar of the appropriate type (light for on-center and dark for off-center) is moved in either direction across the receptive field. However the consistency of response patterns from the two directions of movement may not be present in the cortex since many of the S-cells are direction selective (4).

To help overcome the restrictions resulting from direction selectivity we correlated the response patterns for moving light and dark bars with those obtained when stationary light bars, of similar conformation, were flashed at different points in the receptive field.

ALIGNING RESPONSE PATTERNS TO MOVING BARS AND STATIONARY FLASHING BARS. To make the alignment in the discharge pattern to stationary and moving stimuli it was necessary to take account of the latency of the response to the moving stimulus. A method for measuring this discharge latency (4) is based on the variation in the time of occurrence of the response to a range of stimulus velocities.

The reasoning behind this method is as follows: A thin dark or light bar travels at a velocity, \( v \), and generates a discharge on reaching a point at a distance, \( S \), from the starting point. The interval, \( t \), from the time the bar starts to move to the peak response is composed of the time taken to travel the distance, \( S \), plus the latency, \( t_l \), due to neural processing. Of these two durations, the former is inversely proportional to stimulus velocity, whereas the latter is assumed to be constant under our experimental conditions. Thus

\[
t_l = t - \frac{S}{v}
\]

Expressed as number of bins, \( n \), of bin width, \( b \)

\[
t = nb \quad \text{(with an uncertainty of 1} b\text{)}
\]

If the product \( vb \) is constant then

\[
t_l = (n - A)b
\]

where \( A \) is a constant. Thus, \( t_l \), is derived from the slope of the line that results when \( n \) is plotted against \( 1/b \).

The application of this method of latency measurement is shown in Fig. 4 where it is apparent that the responses of an on-center BS cell to a light bar moving in opposite directions diverged as the stimulus velocity increased and the bin width decreased. The plots of the bin of peak discharge against the reciprocal of the bin width have slopes indicating a latency of 88 ms for one direction and 99 ms for the other.

Latencies were measured for 7 LGN units and 13 S-cells in the striate cortex. Measurements of latency by this method, however, were not always available and it became necessary to know how closely the latency to movement corresponded with the latency to a flashing response from the same region. In 12 of the 13 cases where the two latency measurements were available, they fell within 30 ms of each other and in only one was the difference as great as 50 ms. Since this difference of 30 ms corresponds to less than two bins in most of the time histograms, we judged it appropriate to use the flashing-bar latency to adjust the spatial position of the moving-bar histograms in those instances where direct estimates were unavailable.

Examination of the distribution of latencies of LGN neurons to moving bars showed that they ranged from 60 to 185 ms. For individual cells, the latencies of different peaks varied from one another. The latency of the central peak ranged from 60 to 95 ms, whereas secondary peaks (i.e., dark-bar discharges in on-center units and light-bar discharges in off-center units) had latencies between 140 and 185 ms.
FIG. 4. Determination of the response latency of an on-center BS neuron in the LGN to stimulation by a light bar moving across the receptive field. The average response histograms on the left illustrate the cell’s response to a light bar (0.1 x 0.3") moving at different velocities. Velocities and bin widths are indicated for each group of histograms, 20 stimulus sweeps in each histogram. Plots on the right side of the figure illustrate the variation of the bin number corresponding to the peak response for different velocities. These values are plotted against the inverse of the bin width and the slope of the regression lines give the cell’s latency. For further details see text.

Figure 5 shows the alignment of the response pattern to moving light and dark bars with respect to that of a flashing light bar for two on-center (A and B) and two off-center (C and D) LGN neurons. In all cases the histograms for moving bars have been shifted by the number of bins corresponding to the measured latency and as a result, the moving and stationary response profiles in Fig. 5 are in exact spatial correspondence.

From all the examples in Fig. 5 it is apparent that the central discharge region to the moving bar arises when the appropriate bar (light bar for on-center) travels up the steep, near side of the flashing-light receptive-field profile (cf. Ref. 31). The bar of opposite contrast (dark for on-center) generates a discharge when it descends the far edge of this central region profile. Similar patterns were observed in both BT and BS LGN units, although in some of the larger BT units the response to a moving bar was
FIG. 5. Correspondence between flashing-light field and moving-bar response patterns for on-center (A and B) and off-center (C and D) neurons in the LGN. The average response histograms for light and dark bars have been shifted by a number of bins corresponding to the cell's response latency and the resulting patterns positioned in spatial correspondence with the flashing-bar response field. The flashing-bar response field is made up of the strength of the on-response (thin line) and off-response (thick line) at different positions. The unit of response is the spike per sweep and each sweep is made up of an 0.8-s presentation (on or off) with 1- to 2-s hold times between presentations. The interrupted lines in the flashing bar histograms record the level of spontaneous activity. A: 0.1 x 0.2° moving bar, 20 sweeps at 0.46°/s. B: 0.2 x 0.6° moving bar, 20 sweeps at 1.83°/s. C: 0.1 x 0.5° moving bar, 20 sweeps at 0.46°/s. D: 0.1 x 0.7° moving bar, 20 sweeps at 0.46°/s.
too weak to allow a satisfactory comparison with the flashing-bar pattern.

Excitatory responses may also be elicited from the surround of the concentric LGN receptive field and it cannot be assumed that an excitatory flashing-bar response in the receptive field of a cortical neuron necessarily comes from the center of a geniculate receptive field. We have recorded two instances of LGN units that gave a strong surround response to stimulation with a long bar (see example in Fig. 11B).

In summary, therefore, when the region of most pronounced discharge to flashing bars corresponds with the central component of the receptive field, the appropriate moving bar (light for on-center and dark for off-center) evokes an excitatory response from the near side of the discharge region. The bar of opposite contrast is effective on the far side of this region. Occasionally, a secondary discharge from light and dark bars in on- and off-center units, respectively, appears on the far side of the surround of the receptive field. It is noteworthy that the relative strengths of these discharges vary from one LGN neuron to the next and that the interpretation of S-cell response patterns is complicated by the presence of direction selectivity. The contribution coming from the central component of the LGN neuron receptive field is simpler to identify in non-direction-selective S-cells because the moving-bar discharge regions are symmetrically disposed on either side of the central region of flashing-bar discharge. In the next section we apply these rules to find how the response of monosynaptically driven S-cells in lamina 4 may be linked with their parent LGN cells.

Response patterns of monosynaptic S-cells

In the striate cortex, results were obtained from 50 S-cells, each of which received a monosynaptic input from the thalamus. All these units had receptive fields within 12° of the midpoint of the area centralis. Four cells had end-zone inhibition strong enough to include them in the $S_b$ category (17). Because, in their other receptive-field properties these cells resembled the rest of the monosynaptic S-cells, they were included in this group. Our observations on the strength of the end-zone inhibition in monosynaptic S-cells are described in the following paper (29). The monosynaptic nature and the type of input (BS or BT) received by these 50 S-cells was identified by measuring the latency to electrical stimulation in the afferent pathway after the methods described earlier (6, 7).

From histological reconstruction of the tracks, 43 S-cells were found in lamina 4 or in the lower part of lamina 3; one cell resided in lamina 3 and another in lamina 5. The remaining five cells did not have an electrolytic lesion close enough to be certain of their laminar position, but the depth at which they were recorded suggested that they were located in lamina 4.

In the present study we have excluded S-cells in lamina 6 from the sample population even though some of these cells receive a monosynaptic input from the thalamus (8, 26). In an accompanying paper (29) it is argued that the lamina 6 S-cells also receive a convergent input from other cortical neurons and, thus, are less appropriate than lamina 4 S-cells as representatives of the first stage of cortical processing.

For the comparison with LGN neurons we prepared histograms of the response pattern of monosynaptically driven S-cells to light and dark bars and aligned them, after allowing for the latency of the response, with the responses to stationary flashing bars. Twenty-seven S-cells were examined quantitatively in this fashion and, in an additional 16 S-cells, the flashing-light response was assessed only with hand-held stimuli. In most instances the analysis allowed us to draw conclusions about the nature of the LGN input to the cortical cell. In eight neurons, however, the analysis proved equivocal either because the response to flashing bars was too weak (five cases) or there was poor agreement between regions of flashing-light response and the pattern of response to moving bars (three cases).

The 42 monosynaptically driven cells for which we made an assessment of the organization of LGN input could be classed as receiving their input from: class 1, a single type of LGN neuron (i.e., either on-center or off-center); class 2, two different types of LGN neurons (i.e., one group on-center and
one off-center); class 3, possibly from three groups of LGN neurons (e.g., one off- and two on-center).

The decision about class 3 neurons was equivocal since, in some aspects of their response patterns, these cells would be more appropriately placed in class 1 or 2. The distribution of the 42 units among the three classes was as follows: 10 in class 1; 26 in class 2; and 6 (possibilities only) in class 3. Most units were direction selective although a few neurons with weak direction selectivity were found in each of the three categories.

**MONOSYNAPTIC S-Cells WITH A SINGLE TYPE OF LGN INPUT.** From their response patterns, the input to 10 S-cells was classed as coming from a single type of LGN unit. Figures 6 and 7 show three examples of these S-cells. It is important in examining these response patterns to appreciate the variation in response strength that may occur in cells receiving the same class of input.

In Fig. 6, the histograms in A show the responses to moving light and dark bars while those in B, the response field to stationary flashing bars. The analysis of these responses is simplified by the absence of direction selectivity. The dark-bar discharge regions in both directions occupy the same position in space and correspond to the domain of the off-response to flashing light, a feature characteristic of off-center LGN neurons (cf. Fig. 3). Like LGN off-center neurons, the light bar elicited a discharge that followed the dark-bar response. The similarity of the response pattern of this cortical S-cell to that of off-center LGN neurons is even more evident in Fig. 6C. Here the moving light- and dark-bar responses are shown against background firing that was raised artificially by a monocular conditioning stimulus (18).

The next example of an S-cell with a single type of input, this time from on-center LGN neurons, is presented in Fig. 7A and B. Although this unit was direction selective it was possible to distinguish a response to a light bar in both directions (Fig. 7A). These two responses occupy the same spatial position, which is aligned with the region of on-response to flashing light, thus indicating the presence of an input from on-center geniculate units. The dark-bar response in the preferred direction also came presumably from these on-center units as no off-response was recorded at the same location.

The third example, presented in Fig. 7C and D, displays some unexpected features in its response patterns. This unit was considered to receive its excitatory input from a group of off-center LGN cells, as indicated by the correspondence of the small dark-bar discharge regions in both directions with an off-response to flashing light. The small size
FIG. 7. Response patterns of two monosynaptic S-cells receiving from one type of LGN input: on-center BT (A, B) and off-center BT (C, D). A and C: average response histograms to moving light and dark bars (shifted to compensate for response latencies). B and D: flashing-light response fields. Note dashed line indicates level of spontaneous activity. Stimulus details: A: 0.05 x 2.2° moving bars, 40 (light bar) and 60 (dark bar) sweeps at 1.83°/s. B: 0.15 x 2.2° bar, 12 presentations. C: 0.2 x 2.1° moving bars, 20 (light bar) and 60 (dark bar) sweeps at 3.66°/s. D: 0.2 x 2.1° bar, seven presentations.

of this primary dark-bar response compared to the light-bar discharge was not unexpected, as this had already been noticed in a number of off-center LGN neurons (Fig. 3C, F). The marked strength of the second dark-bar response was not anticipated, however, as no off-center LGN unit exhibited such a strong secondary peak. This response does not appear to arise from the presence of another group of LGN inputs since there was no off-response from this area. A possible explanation for the enhancement of this secondary dark-bar discharge is provided in the DISCUSSION.

MONOSYNAPTIC S-CELLS WITH TWO TYPES OF LGN INPUT. Twenty-six S-cells exhibited response patterns consistent with the idea that they received their excitatory input from two types of LGN neuron—one on-center and the other off-center. Figure 8A shows the responses of such a putative double-input cell to moving light and dark bars, Fig. 8B its responses to a stationary flashing bar, and Fig. 8C its responses to moving bars in the presence of a monocular conditioning stimulus. Note in Fig. 8C that the starting point of the bar was displaced with respect to that in Fig. 8A, so that spatial correspondence is lost between these two graphs.

In the histograms in Fig. 8A there are two bidirectional discharge regions, one to a light bar and the other to a dark bar. Each of these discharge regions aligns with a corresponding region in the flashing light field (i.e., the light bar with the on-region and dark bar with the off-region). It would appear, therefore, that this cell received its input from two types of LGN neuron and that the two groups had receptive fields arranged in tandem in the direction of movement, at right angles to the optimal orientation.

Since each LGN unit generated at least two discharge regions to bars moving in each direction (one to a light and one to a dark bar) we expected, but did not see, four discharge regions in the receptive fields of S-cells receiving a dual type of input. An explanation for this apparent restriction is that the middle pair of the four expected discharges merged with one another. For example, in the upper histogram in Fig. 8A the dark-bar discharge from the on group could combine with that from the off group, and in the lower histogram when the direction of movement is reversed the light-bar discharge of the off group could combine with that of the on group. These features, which were found in all our dual-input S-cells, are even more clearly demonstrated in Fig. 8C, which illustrates the responses to light and
dark bars in the presence of a monocular conditioning stimulus.

Three more examples of S-cells receiving an input from two types of LGN neuron are included to give some idea of the variability within this group. The first two of these cells, the ones in Fig. 9A and B, are direction selective in their response patterns. In both these units it was not possible to recognize the centers of the afferent LGN units from the pattern of moving-bar discharge alone, since there was no bidirectional discharge region. However, the finding that the flashing-light response was as strong for the on- as it was for off-response suggests the presence of two types of LGN input.

For the cell in Fig. 9C the response to the dark bar was totally direction selective, while there was only a slight directional preference in the response to the light bar. These moving-bar discharge regions correspond with the appropriate regions of flashing-light response. The strength and short latencies of the flashing-light responses are characteristic of a center-component response in the LGN (9). We concluded, therefore, that each of the two peaks in the flashing-light response field corresponded to a group of LGN receptive-field centers.

**SEPARATION OF DISCHARGE REGIONS IN DUAL-INPUT CELLS.** The merging of moving-bar responses in cells with a suspected tandem arrangement of LGN inputs suggested that a small separation existed between the two elements of the tandem. Direct measurements of the distance between the discharge peaks in the flashing-light receptive field allowed a more accurate estimate of this separation. It is now known, for units of similar retinotopic position, that BS neurons in the LGN have smaller discharge centers to flashing stimuli than BT neurons (9, 11, 21). Once the afferent pathways to S-cells had been identified it was possible to see if these size differences in the LGN receptive field were reflected in the separation of the two regions of flashing-light response in S-cells.

For such an analysis we measured the receptive-field centers of LGN units by plotting the length-response curve for moving bars of contrast appropriate to the center

**Fig. 8.** Response patterns of a monosynaptic S-cell receiving from two groups of LGN BS neurons. A: histograms to light and dark moving bars (shifted to compensate for response latencies); B: flashing-light response pattern; and C: response histogram to moving light and dark bars in the presence of a monocular conditioning stimulus. Section C not in spatial alignment with sections A and B. A: 0.1 x 0.3" moving bars, 20 sweeps at 0.46°/s. B: 0.1 x 0.5" flashing bar, five presentations. C: 0.1 x 0.5° moving bar, 40 sweeps at 0.46°/s.

(i.e., light for on-center, dark for off-center) and then determined the length of bar at which summation ceased (cf. Ref. 29). The results of this evaluation, plotted in the scattergrams in Fig. 10A and B, show the distribution of receptive-field diameters of LGN units (open circles) plotted against their eccentricity in the visual field (16 BS units in A and 19 BT units in B). Also in Fig. 10,
FIG. 9. Response patterns of three dual-input monosynaptic S-cells (A: BT input; B: BS input; C: BT input). In A and B the moving bar histograms are positioned above the flashing-bar response fields. In C, the order is inverted and the filled histograms illustrate representative flashing-light responses. Note: dashed line indicates level of spontaneous activity. Stimulus details: A: 0.1 x 1.5° moving bars, 20 sweeps at 0.92°/s; 0.1 x 1.5° flashing bars, 10 presentations. B: 0.05 x 3.5° moving bars, 40 sweeps at 1.83°/s; 0.1 x 3.5° flashing bar, 20 presentations. C: 0.15 x 3.5° flashing bar, 10 presentations for the response field, 60 and 80 presentations for the dark histograms; 0.05 x 3.5° moving bars, 40 sweeps at 1.83°/s.

we have plotted (filled circles), for S-cells with a presumed dual input, the separation between peaks of on- and off-discharge. Those cells with drive from BS units are in Fig. 10A and those whose drive comes from BT units are in Fig. 10B.

It is evident that the points representing cortical and LGN units distribute over equivalent regions in the two scattergrams of Fig. 10. This result suggests that the midpoint of the flashing-light discharge regions of S-cells are separated by a distance equivalent to the diameter of the receptive-field center of the contributing LGN neuron and, therefore, that the two elements of the tandem are juxtaposed with little or no overlap. MONOSYNAPTIC S-CELLS WITH INPUTS FROM THREE GROUPS OF LGN CELL? If it is assumed that the response from the surround of an LGN neuron is not apparent in the flashing-light field of an S-cell, then it can be argued that there are six S-cells that receive their input from three groups of LGN neurons. This decision was based on the presence of three neighboring regions in the flashing-light field of these S-cells. However, the response pattern of the moving light and dark bars generally failed to meet the expectations of such a tripartite organization. The response patterns of a neuron possibly receiving a trio of inputs are presented in Fig. 11A.
FIG. 10. Comparison between the receptive-field center sizes of LGN units and the distance separating the two sets of inputs into dual-input monosynaptic S-cells. The receptive-field center size is taken as the summation length (see text and Ref. 29). For cortical units, the center-to-center distance was measured as the distance between the peaks of off- and on-response in the flashing-light response fields (see examples in Figs. 9 and 10).

The lower part of Fig. 11A, shows the response patterns to moving light and dark bars and, above them, the flashing-bar response field. It is apparent that while the central on region aligns with a bidirectional discharge to a moving-light bar, the two off regions correspond only to the unidirectional dark-bar discharge region. Indeed, the moving bar response pattern is reminiscent of that of S-cells with a single type of LGN input, where the two off regions would be attributed to the surround of the afferent LGN receptive field. This possibility is supported by the occasional observation of tripartite fields in LGN neurons (Fig. 11B) particularly when long (1–3°) bars were employed as stimuli. (The bar lengths used on the six S-cells with three divisions in their flashing-light receptive fields ranged from 1.5 to 4.5°.)

To identify the origin of discharge regions in the flashing-light receptive field of S-cells it is necessary to distinguish the contribution coming from the center and the surround of LGN receptive fields. There seems little doubt from examples of LGN units (Fig. 11B) that the surround response, particularly to long bars, may be strong enough to activate cortical cells. However, temporal differences in the center and surround responses, possibly due to the relative suitability of the stimulus, help to identify these two components. The LGN BS unit in Fig. 11B follows the general rule of the surround latency being longer than that from the center. Testing for this distinction in four of the six S-cells with tripartite fields we found, for each one of them, a long response latency in at least one of the outer discharge regions. This latency was in excess of 200 ms and was, therefore, unlikely to be derived from the center of a contributing LGN receptive field. Discharges from the three regions in the flashing-light field for one of these cells is shown in Fig. 11A; the latencies measure 85 ms for the central on-response and 115 and 205 ms for the off-responses in the outer discharge regions. This result is to be contrasted with that recorded from the two discharge regions of S-cells with a dual input where the latencies were similar to each other and less than 150 ms.

The four S-cells that could have received a trio of LGN inputs, for which we tested the latencies to flashing light, were all found to have long-latency discharge regions similar to those of the cell in Fig. 11A. The question of whether S-cells ever receive a
FIG. 11. Response patterns of A: monosynaptic S-cell with BT input; and B: LGN BS unit. For both units, the histogram to moving dark and light bars are placed at the bottom of the figure. The flashing-light response fields are presented above with examples of the flashing-light response from different parts of the field. Broken line indicates level of spontaneous firing. Stimulus details: A: 0.1 x 2.2” moving bar, 20 sweeps at 3.66”/s; 0.15 x 1.4” flashing bar, eight presentations; presentations for filled histograms (left to right): 260, 40, 60. B: 0.1 x 0.3” moving bar, 20 sweeps at 0.92”/s; 0.1 x 1.7” flashing bar, five presentations; presentations for filled histograms (left to right): 60, 40, 40.

Drive from three different groups of LGN neurons will be considered in the DISCUSSION.

LATERAL EXTENT OF RECEPTIVE FIELDS OF S-Cells. So far, we have considered the organization of S-cell receptive fields along the perpendicular to the cell’s preferred orientation; now we turn to the line parallel to this orientation. We have estimated the lateral extent of the receptive field from the point where the cell ceases to demonstrate any further summation in the length-response curve (see above and Ref. 29). By comparing the summation length in the two types of S-cell (in the fast and slow streams) with a similar measure made in the LGN BT and BS units, respectively, we hoped to determine the amount of overlap that might arise from the convergence of LGN inputs. In Fig. 12A a comparison is drawn between the summation length of S-cells of the slow stream and the diameter of receptive-field centers of BS cells in the LGN, while Fig. 12B duplicates this plot for fast-stream S-cells and BT LGN neurons. As a population, the S-cells show a greater lateral dimension than would be anticipated from the contribution of a single LGN neuron. Domains can be established to encompass a
FIG. 12. Comparison of the summation lengths for BS and BT units and the first-order S-cells receiving their input from these two groups of neurons. For definition of summation length see text.

large proportion of the points representing the two populations (approximately 80% between bracketed arrows in Fig. 12A and 90% in Fig. 12B).

It follows from examination of Fig. 12 that, in their lateral extent, S-cell receptive fields are equivalent to twice the diameter of receptive-field centers of the parent LGN neurons. This relationship is evident in the fact that it requires a shift of a factor of 2 (on the logarithmic scale) to superimpose the domain of cortical cells onto that of LGN neurons.

SPATIAL ORGANIZATION OF INHIBITORY INPUTS TO MONOSYNAPTIC S-CELLS. In the four examples of monosynaptic S-cells with a balanced input from the two eyes, binocular conditioning (to create background firing) was used to reveal the receptive-field inhibitory zones (18) generated at the cortical level. Examples of the responses with monocular and binocular conditioning are shown in Fig. 13. These examples demonstrate that there is often a strong inhibitory interaction in first-order S-cells and that the inhibitory zones are strictly localized on either side of the excitatory regions. In addition, histograms not presented in this paper show that the inhibition from these regions may be contrast specific.

DISCUSSION

The present study has led to the development of several ideas about the internal structure of the receptive fields of first-order S-cells in lamina 4 of the striate cortex. Many of these concepts have come from establishing parallels between the response patterns of S-cells and their afferent cells in the LGN and much of the discussion is a commentary on these similarities. Regard is also given to response-pattern modifications that appear to occur in going from neurons in the LGN to S-cells in the cortex. From this analysis of response-pattern kinship an attempt is made at the end of the discussion to construct a model to describe the way LGN neurons contribute to the receptive fields of S-cells.

Our observations on the response patterns of LGN neurons confirm the results reported by previous investigators for LGN and retinal neurons (15, 33, 34) and are compatible with the theoretical analysis of these responses by Rodieck (31). In this respect it is interesting to note that the discharge to a moving bar of inappropriate contrast for the receptive-field center (dark bar for an on-center cell, light for off-center) arises as the stimulus crosses the falling side of the profile of the receptive-field center and does
FIG. 13. Average response histograms recorded in the presence of a conditioning stimulus to elevate background firing. A: response of an S-cell with BT input to moving light and dark bars in the presence of monocular conditioning. B and C: responses of two other S-cells in the presence of binocular conditioning. Stimulus details: A: 0.1 x 2.9° moving bars, 60 sweeps at 1.83°/s. B: 0.1 x 2.5° moving bar, 100 sweeps at 0.92°/s. C: 0.2 x 4.5° moving bar, 80 sweeps at 1.83°/s.

not come from stimulation of the antagonistic surround. The antagonistic surround may be the source of the second discharge to a bar of contrast appropriate to the center. The rarity and variability of this response, however, precluded its detailed examination.

As with other investigations into the responses of LGN neurons to moving bars (15) we found a similarity in the response profiles for brisk sustained and brisk transient cells (X and Y in the terminology of Dreher and Sanderson (15)). This similarity in the response to moving bars holds in spite of differences, such as variations in persistence and linearity observed in the responses to flashing stimuli (9, 11, 14, 21). There are, however, quantitative size differences to be observed in individual components of the moving-bar response pattern. The extent to which these differences are handed on to recipient S-cells in the striate cortex is examined in the accompanying paper (29).

The response patterns of almost all the monosynaptic S-cells to light and dark bars moving in the preferred direction could be predicted from combinations of discharges given by the sets of LGN inputs. These combinations were not simple replications of the LGN inputs. In the case of dual-input S-cells, the moving bars gave three successive discharges, the middle one resulting from the merging of like responses from the two adjacent sets. Even for the group of S-cells with one input type there were three examples that displayed discharges to the moving bars that were not anticipated from the response patterns of contributing LGN inputs. For example, if the input to the cell of Fig. 7C is a single group of off-center LGN neurons, then the discharge sequence in the preferred direction (to dark bar, light bar, and then dark bar) conforms to the expected pattern. The unexpected feature is to be seen in the second discharge to the dark bar, which (though usually the weakest) is here much stronger than the primary dark-bar discharge. In the absence of any correlate in the flashing-light discharge, the increased size of the secondary dark-bar discharge appears to be due to cortical enhancement rather than the contribution from another group of LGN units. A possible explanation for the strengthening of this secondary dark-bar discharge is that it comes from firing associated with release from inhibition (2, 24). This could be generated by a group of on-center LGN neurons with receptive fields superimposed on those of the excitatory off-center inputs. If this type of explanation is valid then inhibition may play a significant role in the determination of the relative strength of individual discharges.
In a number of instances the decision that monosynaptic S-cells receive their input from one, two, or three groups of LGN neurons rests on evidence obtained by flashing-light stimuli. This was particularly the case when direction selectivity made it difficult to interpret the way in which the LGN input was arranged to produce the response to moving bars. There is some danger in relying on flashing fields, however, since the surrounds as well as the centers of geniculate neurons are sometimes capable of producing a strong excitatory response when stimulated by long bars (Fig. 11). To avoid this possibility we used short bars (<1°) in most flashing experiments, thereby diminishing the likelihood that the S-cell response came from the surround of an LGN receptive field. Three was the maximum number of well-defined flashing-bar discharge regions found in the receptive field of any first-order S-cell and, therefore, three is also likely to be the greatest number of types of input coming from LGN neurons to the S-cell. The validity of this figure of course requires that no discharge region be overlooked; and we have attempted to reduce this possibility by using the most appropriate stimulus to activate the central receptive-field component of LGN neurons. To this end we selected short and thin bars that were unlikely to cause strong activation of the antagonistic surround and yet were close to the optimal length for the central discharge region of LGN neurons.

It is also possible that inhibition will influence the pattern of discharge peaks seen in the responses of S-cells. These cells frequently have zones of intense inhibition flanking their discharge regions and a release from this inhibitory influence may lead to enhancement of the response contributed from the surround of an LGN receptive field. In addition, excitatory inputs may also be hidden or inhibited so that they only become manifest when the inhibitory influence is removed. Thus, Sillito's (36) finding that a simple-cell receptive field, with discrete areas of on- and off-discharge, is replaced by a single response of composite on/off firing in the presence of bicuculline can be interpreted as the uncovering of an excitatory discharge (46, 47). However, the use of the conditioning technique to create background activity in the S-cell revealed very few sub-liminal or concealed discharge peaks and there is justification for believing that our results are only rarely disturbed by such an input.

Other investigators have described simple cells with receptive-field properties compatible with one or two sets of inputs (40, 43). Toyama, Maekawa, and Takeda (43) have also reported on the possibility of S-cells with three groups of inputs. However, in this study, tests were not carried out to exclude the possibility that surround responses from the LGN might be contributing and there must be some doubt concerning the existence of this type of S-cell. In our sample all the S-cells that could be regarded as possible recipients of a trio of inputs had one discharge region with a long-latency response that was unlikely to have come from the central component of an LGN neuron. In all of the six examples, the number of discharges caused by moving bars was more in keeping with one or two, rather than three, sets of inputs. Another feature of the responses of those neurons that may be considered as candidates for a three pronged input was the strong inhibitory bands that corresponded with the outer region of the flashing-light discharge field. Once again the release from inhibition may lead to an enhanced response from the surround of the LGN receptive field, making it appear as strong as that coming from the center. In the presence of this possibility we believe that the existence of S-cells with a tripartite input must be regarded as unproved.

From the measurements of summation lengths and the distance between discharge regions in the receptive field of monosynaptic S-cells in lamina 4 we conclude that the region of discharge extends over a distance equivalent to two LGN receptive-field centers. This appears to hold both in the direction of optimal orientation and also orthogonal to it (see Figs. 10 and 12). Anatomical support for this interpretation comes from the observation that the terminal arborization of geniculate afferents extends over a distance equivalent to approximately two LGN receptive-field centers (8, 16).

To achieve cortical summation over two LGN center diameters along the line parallel to the optimal orientation, it is necessary to have a scatter of afferent centers such that
their midpoints distribute over one LGN center diameter. In other words, this scatter extends over an average distance of 0.4° for BS units and 0.8° for BT units (Fig. 12). Assuming a unidimensional magnification factor of 0.8–1.9 mm/deg (45) within 8° of the line of sight (as in our sample), then 0.4° represents about 0.5 mm and 0.8° corresponds to about 1.0 mm along the cortical surface. Not only are these values of the same order as those recorded for the terminal spread of LGN axons, but they also come close to the axonal spread of spiny stellate neurons commonly regarded as a prominent first-order neuron in lamina 4 (25, 28). Since this dimensional consistency holds for both types of afferent stream (BS and BT from LGN), it appears as if an organizational principle is at work. Within this design, the size of the LGN receptive-field center appears to exert a determining influence and it would be informative to know if the receptive-field components of S-cells change, along with the LGN receptive-field center size, for more eccentric representations in the visual field. Such a result would be in keeping with the concept of a crystal design advanced for the striate cortex by Hubel and Weisel (23).

Our knowledge of the scatter of the midpoints of the receptive fields of LGN neurons in lamina 4 S-cells is less certain in the line perpendicular to the optimal orientation. It is known, however, that the discharge regions of the flashing and moving bar have a small expanse in this direction and two models may be developed to allow for this and the other findings referred to above. The row model of Hubel and Wiesel (22) provides one answer even though, according to our data, the rows would be quite short. The second model allows for the possibility that the tightness of the discharge regions could also be achieved in a situation where a large scatter of inputs is compensated for by inhibitory mechanisms.

Imagine, for the S-cell receiving a dual input, that the midpoints of the receptive fields of each set of afferent neurons scatter in a circle of diameter equal to a single LGN receptive-field center. By a mechanism of antagonism between these two sets, the discharge regions from both could cancel out in the region of overlap to produce the elongated shape seen in our results. Our data on first-order S-cells do not enable us to choose between this and the row model, but several recent reports (3, 38, 44) indicate that, in the absence of inhibitory mechanisms, the receptive fields of simple (or S) cells display circular symmetry. These results, if they apply to first-order S-cells, are in keeping with the second model and suggest that the LGN inputs have receptive fields that scatter in circular areas instead of aligning in rows.

In order to estimate the maximum number of LGN neurons making up one set of inputs to a monosynaptic S-cell, we will assume (as proposed above) that the receptive-field midpoints of these LGN units are scattered within a circle (of diameter equal to one LGN receptive-field center). It is unlikely, however, that all of the neurons would contribute equally to the firing of the S-cell, since this arrangement would lead to an almost total overlap of light- and dark-bar discharge regions. LGN neurons having their midpoints near the center of the cluster are likely to make the greatest response contribution. If it is assumed that the inputs to the S-cell may be described in terms of a bivariate Gaussian distribution, then we can allow for this in multiplying the area of scatter in the cortical unit by the densities of receptive-field midpoints for LGN neurons. The density values for LGN neurons are derived from the findings of Peichl and Wässle (30) for ganglion cells in the retina. Since there is a similarity of receptive-field sizes in retinal ganglion cells and LGN neurons (10, 12, 21) it is reasonable to equate the densities of these two cells. From Peichl and Wässle's values for α and β ganglion cells (presumed to correspond to BT and BS cells, respectively), it may be said that there are 1.9–8.5 BT cells and 33–330 BS cells per degree squared in the LGN. Assume that there are as many on-center as off-center neurons in the BT and BS populations and that 0.4° is the average figure of the receptive-field-center diameter of BS units and 0.8° for BT neurons. Then, we estimate that the number of LGN neurons supplying each set in the S-cell receptive field corresponds to 2–20 for BS neurons and 1–2 for BT neurons.

The calculated values above correspond to the maximum number of neurons whose
excitatory responses eventually reach the S-cell but they do not distinguish the number of LGN units directly synapsing on this neuron. This number has been estimated to be between 3 and 5 from intracellular recordings (1, 13). The finding that the lamina 4 spiny stellate neuron in mouse somatosensory cortex receives only 48 excitatory synapses from the thalamus (46) is consistent with the idea that there are a small number of direct thalamic terminations on first-order neurons in lamina 4 in all regions of sensory cortex.

Our study of the excitatory responses of monosynaptic S-cells has led us to the conclusion that many of their receptive-field properties can be explained by assuming that they receive their major excitatory drive from one or two sets of LGN neurons, with each set containing a maximum number of 30 elements of like type. This approach, however, falls short of explaining the mechanisms of orientation and direction selectivity in first-order cells. Clearly, the inhibitory components of the receptive field hold the key to the understanding of these mechanisms and further studies should be directed to evaluating the interplay of excitatory and inhibitory influences in shaping these selective features in the responses of first-order S-cells.

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