Response Characteristics of Single Neurons in the Rabbit Visual Cortex

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Unitary discharges were extracellularly recorded from cortical cells in the rabbit's visual area. Most of the cortical units were responsive to large-field illumination which was turned on and off at about 0.8/sec. Response characteristics of cortical cells were largely similar to those of retinal ganglion cells. One hundred and twenty-nine units which were analyzed successfully were categorized into four classes according to the features of their receptive fields: simple, asymmetric, complex and compound. Especially, compound receptive fields were so named on the basis of the finding that the whole receptive field consisted of three separable complex fields.

A columnar arrangement of cortical neurons was suggested on the basis of the fact that the localization of the receptive fields of units involved in a particular column was almost identical in the visual field. No other common properties to specialize the column was detected. Most of the receptive fields of units which were localized in the visual streak were oval in shape with their long axis horizontal as described in retinal ganglion cells. It is likely that in the rabbit's visual cortex no more elaborate analysis is made on in-coming visual information, but rather some integrative action is carried out for further processing.

Recent investigations on response characteristics of the retinal ganglion cells in the rabbit have revealed that considerable analytical processing on visual information is achieved at the level of the retina in this animal.1-4 This is in striking contrast to the cat and the primates, in which such processing is achieved at the level of the cerebral cortex.5-7 In this connection the simplest question to be raised is what sort of further processing is carried out in the primary visual cortex of the rabbit.

In the lateral geniculate body of the rabbit, Arden8-10 described various receptive field organizations which were quite different from simple concentric organizations found in cat's retinal ganglion cells11 and lateral geniculate neurons.12,13 The complex receptive fields as described by Arden might have been predicted in the light of the present knowledge on properties of retinal ganglion cells which were investigated in detail by Barlow and his coworkers1-4 anatomical evidence on the convergence of the optic nervesfibers to a geniculate neuron.14
The main object of the present investigation is to answer the above-mentioned question. The results indicate that response characteristics of visual cortical neurons are largely similar to those of retinal ganglion cells. Cortical neurons do not effect further analytical processing on the visual information conveyed along the specific afferent fibers, but rather exert some integrative action on it.

Our results are similar to those recently published by Arden et al.\textsuperscript{15}

\section*{Method}

Twenty-one albino rabbits, weighing from 2.5 to 3.5 kg, were used in these experiments. They were initially anesthetized with pentobarbital sodium (30 mg/kg) injected intraperitoneally and during the experiments immobilized by means of a continuous intravenous infusion of gallamine triethiodide at a rate of 20 mg/hour in 5\% glucose solution (2 ml/hour). The animals were firmly fixed to a head holder and maintained on artificial respiration.

The skull was opened wide enough to expose the whole drosal aspect of the visual cortex. The dura mater was cut away, and the exposed brain was covered with warm soft paraffin (melting point, 40\degree C) to prevent drying and cooling. Cisterna magna was usually opened and drained to minimize unfavorable movements of the brain.

The eye contralateral to the exposed cortex was confronted to a white tangent screen standing one meter from the animals and roughly normal to the pupillary axis. The pupils were dilated with cyclopegic mydriatic (Midrin-P), and the corneas were covered with plastic contact lenses of appropriate power. The power of the lenses was determined by means of a streak retinoscope, so that the tangent screen was focused onto the retina. It usually ranged from 5 to 7 D for normal adult rabbits.

Visual stimuli were displayed on the tangent screen and all characteristics of receptive fields were recorded on a sheet of paper attached to the screen. Usually the screen was diffusely illuminated with a tungsten lamp from above which could be driven intermittently at about 0.8/sec or steadily. The steady illumination of the screen served as background illumination of 2 cd/m\textsuperscript{2} throughout the experiments. For mapping receptive fields a flashing circular spot of light delivered from a glow modulator tube (Sylvania R 1131 C) was shown on the screen. The diameter of the spot was 1/3\degree of visual angle, its luminance being 20 cd/m\textsuperscript{2}. For further specification of receptive fields a thin slit of light (1/10\degree x 2\degree) delivered from a streak retinoscope and various patterns of visual stimuli projected from a slide projector were flashed on and off or moved back and forth on the screen. The speed of moving stimuli was estimated by measuring time interval between two output signals from two photo diodes, separated from each other by 10\degree of visual angle on the screen over which visual stimuli passed.

All receptive fields were mapped out with respect to the optic disc and the large blood vessels which travel a reasonably straight course over the medullary rays.\textsuperscript{16,17} They were projected and drawn on the screen by means of a narrow beam ophthalmoscope which was in principle similar to that used by previous workers.\textsuperscript{7,18}

Action spikes were recorded with tungsten microelectrodes insulated with Formvar enamel except at the tip. Electrodes were advanced as perpendicularly as possible to the cortical surface by means of a hydraulic micromanipulator fixed in the head holder. Spikes were amplified with a conventional RC amplifier with a cathode follower input stage, displayed on the cathode ray oscilloscope screen and photographed on 35 mm x-ray film.

Body temperature, measured under the scapula with a thermister thermometer, was held at 37.5\degree C with an electric heating pad placed under the body.

When the experiments were terminated, animals were sacrificed and perfused via the aorta with warm physiological saline followed by 10\% formalin. If necessary, electrolytic lesions were made to check the position of the tip of the electrodes by passing
100μA direct current for 10 sec with the electrode positive. The brains were sectioned at 30μ on a freezing microtome and stained with cresylviolet.

RESULTS

The visual cortex was explored according to a chart of projection of visual field on the rabbit’s cerebral cortex which was constructed in our laboratory on the basis of unitary activity of cortical neurons in response to a small spot of light displayed on the visual field. This chart (to be published in Tohoku J. exp. Med.) is slightly different from that which Thompson et al. made with photically evoked potential as an index.

The electrode was lowered carefully, watching the CRO screen and listening to an auditory monitor, into the cortex through the paraffin layer stuffed in the opening of the skull. The cortical surface was easily detected by a sudden reduction of noise and of electrical resistance of the electrode. The depth of a unit recorded was measured with reference to this surface on the readings of the scale of the micrometer which drove a hydraulic micromanipulator. On noticing any sign of an isolated action spike during a penetration, the advancement of the electrode was stopped and held still for one or two minutes until the magnitude of the action potential grew large and its wave shape showed positive-negative sequence. Usually a stable large spike of positive-negative configuration was obtained during this time, but sometimes units were lost without any sign of damage or with signs of injury.

In the present experiments 129 soma units were recorded and analyzed successfully. The identification of soma units was exclusively based on the wave shape of their action potentials. Positive-negative biphasic configuration with an inflection on a rising positive phase and relatively long duration of action spike were two major criteria used. The amplitude of action spikes ranged from 200 μV to 5.0 mV.

Response characteristics of cortical neurons

In rabbits, most of cortical cells were responsive to turning on and off diffuse illumination of the white tangent screen. This was in striking contrast to cat’s neurons in the visual cortex which were entirely insensitive to such diffuse illumination.

Units were examined for their ‘trigger features’ by moving to and fro various patterns of visual stimuli or turning on or off stationary visual stimuli. 129 units were tentatively classified into the following categories (Fig. 1).

1) simple units
2) units of asymmetric fields
3) complex units
4) compound units

Simple units. The receptive fields of simple units were easily outlined by
Fig. 1. Classification of cortical neurons in the rabbit's visual area.

Under each heading, the receptive field of that type is illustrated: ○ stands for on response to stationary spot of light, △ for off response, and ⊙ for responses both at on and off.

An arrow indicates the preferred direction of movement of a target to which the unit responded most actively. Figures in the third row give the number of units observed, among which the number of units which showed directionally selective property is given in (the subsection of the third row, indicated by dir. sel.)

Of 38 complex units 10 were responsive only to a thin slit of light, 18 responsive only to a black target and 10 responsive to unclassified patterns of stimuli. The sample was 129.

observing responses to a small spot (1/3° of visual angle in diameter) of light flashed on and off. They were usually oval or round in shape and could be further classified into ‘on-center’, ‘off-center’ and ‘on-off’ fields according to whether they responded to the light spot centered at the center of the receptive field at on, off and at both on and off, respectively.

‘On-center’ and ‘off-center’ receptive fields were largely similar to concentric fields described in rabbit’s retinal ganglion cells. The surround of the opposite phase response within receptive fields was hardly detected in these units as in retinal ganglion cells. The ‘on-off’ receptive fields were characterized by on-off responses over the whole receptive field with no center-surround organization detected.

a) ‘On-center’ and ‘off-center’ units. An example of simple ‘on-center’ units is illustrated in Fig. 2. The receptive field mapped out by a flashing spot of light (2° of visual angle) was oval with its long axis oriented horizontally. The light spot placed at the center of the receptive field produced an acceleration of discharge (on response) as long as the light shone. Increase in the size of spot elicited a stronger discharge, but as the size exceeded that of the receptive field the response became weaker. This finding indicates that there is an inhibitory region surrounding the receptive field.

Moving of the spot of light across the receptive field elicited a response as well. A stronger response was observed to the centripetal movement of the light than to the centrifugal one. Furthermore, the unit responded to a moving small black
Fig. 2. Simple 'on-center' unit.

Oval-shaped receptive field was located in the visual streak. a: responses to a flashing spot of light (2° in diameter and 20 cd/m² in luminance) centered in the receptive field. b and c: responses to the same spot of light moved along long axis and short axis of the receptive field respectively, speed of movement being given beside each figure. d: responses to a spot of light just as large as the receptive field. e and f: responses to a small black target (2° in diam.) moved across the receptive field. g: responses to rather large black target which was moved into, stayed for a little while and then moved out of the receptive field.

Object (2° of visual angle). When the black target was brought into the receptive field center, the on-going discharge was suppressed and as the target was moved out of the field the initial on-going discharge was recovered. Such a behavior of the unit in response to a moving object is predictable on the basis of functional properties of the concentric organization of mutual antagonistic regions.

In addition to such a simple 'on-center' unit some 'on-center' units were found to have a directionally selective property, as reported in retinal ganglion cells. An example of these is shown in Fig. 3. This unit responded to a small spot of light (1/3°) only when it was flashed on within its receptive field (bottom trace in Fig. 3). The off-surround could not be detected by a flashing spot method. The contour of the receptive field is shown by a continuous line with crosses which indicate no responses to the flashing light at all.

When the spot of light was left on and moved in various directions across the receptive field, it was observed that the unit gave a strong discharge to upward movement along the oblique axis through the receptive field (preferred direction), but no response to downward movement (null direction) along the same axis. The preferred direction is indicated with a thick arrow-headed line and the null
The exploring spot of light (1/3° in diam.) centered in the receptive field produced on response (bottom trace), where upward deflection of light stimulus marker indicates light on and downward deflection light off. The preferred and null directions are indicated by continuous and broken arrow-headed lines, respectively. a, b, c and d stand for minute movements of the spot of light within the receptive field. Horizontal and vertical directions in the visual field and angular size scale are shown below in the right.

direction with an arrow-headed broken line. It should be mentioned here that this unit had another preferred-null axis perpendicular to the above-mentioned axis. The spot of light moved along this axis elicited discharge of spikes when the movement was in antero-posterior direction but no response was produced to the movement in the reverse direction. In the intermediate directions no preferred-null property was gained.

The direction-selective property was proved in the same axis for a black object moved on a white background as well, and also for minute movements anywhere within the receptive field. The most sensitive part to the movement was found at the center of the receptive field.

The above-mentioned properties were concerned with ‘on-center’ units but similar properties were also observed in some of ‘off-center’ units. The directionally selective property was demonstrated in 9 of 40 ‘on-center’ and 5 of 23 ‘off-center’ units.

b) ‘On-off’ units. ‘On-off’ units, as categorized here, gave on-off responses to a flashing spot of light anywhere within their receptive field. Responses were not so crisp in these units and in general their receptive fields were found larger than those of ‘on-center’ and ‘off-center’ units (Fig. 4). It was surprising that most of ‘on-off’ units were not directionally selective in contrast to the fact that in retinal ganglion cells ‘on-off’ units were predominantly directionally selective. Only one of 17 units was found to be directionally selective.
Fig. 4. Distribution of the diameter of the receptive field of 'on-center' 'off-center' and 'on-off' units. The diameter was measured by intermediate value between the longest and the shortest axis lengths.

Units of asymmetric field. A unit illustrated in Fig. 5 had an asymmetric organization of the receptive field as mapped out by a flashing spot of light. The contour of the receptive field is oval with its long axis in the horizontal direction. A large part of the receptive field was occupied by an on-off region (denoted by ⊙) and small on and off regions were located separately in the periphery. The unit gave a brisk discharge to a slit of light (1/10°×5° of visual angle) oriented vertically.

Fig. 5. Unit of symmetric field.

The central part of the receptive field gave on-off response to a small stationary spot of light and on and off regions are located in periphery separately. A slit-shaped light stimulus vertically oriented produced brisk response when moved horizontally in the antero-posterior direction, but weak response in the reverse direction. The orientation of the axis of the receptive field is considered vertical.
when moved in the antero-posterior direction, but a weak response to movement in the reverse direction. To vertical movement of the slit of light oriented horizontally it responded to an almost equal degree in either upward or downward direction. It is clear that the asymmetric organization of the receptive field is responsible for asymmetric responses to the moving stimulus.

**Complex units.** Units involved in this category were characterized by the findings that they gave no response or unstable responses to stationary light stimuli, whereas they responded with brisk discharge to specialized types of stimuli. Fig. 6 shows an example of complex units. The contour of the receptive field of this unit was hardly determined by the flashing spot method. The unit responded to a slit of light and also to a black bar oriented horizontally only when it was moved vertically. It is to be noted that the unit gave a weak response to the light stimulus moved across the receptive field all the way through, while brisk discharges were elicited by the light moved up and down within the receptive field. The black bar could evoke brisker discharges in either way of movement. On the contrary the vertically oriented stimuli of the same kinds were

![Image](image.png)

Fig. 6. A complex unit.

Horizontally oriented luminous and black bars (1/4° × 2.5°) were found to be adequate stimuli when they were moved up and down vertically across the receptive field. This unit did not respond to a stationary spot of light flashed on and off, so that the receptive field was outlined on the basis of responses elicited by the above-mentioned stimuli. Top record shows that spike discharge is not related to flashing light centered in the receptive field. Lower trace of this record indicates light mark where upward and downward deflections correspond to ‘on’ and ‘off’ of light respectively. The upper record of the two in the black bar and light strip columns shows spike discharges evoked by the stimuli moved across the receptive field all the way through, and the lower one discharge patterns in response to the stimuli moved up and down within the receptive field. Two records at the bottom show spike discharges concerned with vertically oriented stimuli moved horizontally. In these records the lower traces indicate output signal of the photodiode placed at the center of the receptive field, where upward deflection indicates the moment the light strip passed by the photodiode. Depth of the unit in the cerebral cortex was 1.5 mm.
entirely ineffective to evoke discharges. Such behavior of this unit might be accounted for by the existence of a strong inhibitory area surrounding the receptive field. Actually the response elicited by the above-mentioned way was suppressed by the simultaneous display of another slit of light in the surrounding region.

Another example of complex units is given in Fig. 7. This unit was almost silent under ordinary conditions and also when the background illumination was turned on and off. Various patterns of visual stimuli were tried to evoke any response from this unit, until an arrow-headed black object was found to be effective. The unit responded to forward movement of this stimulus directed anteriorly but not to the opposing movement. The receptive field was not determined anyway. Such a peculiar unit was so rarely encountered that further details of its characteristics could not be checked.

![Fig. 7. A complex unit.](image)

Effective pattern of stimulus was ultimately found to be a black arrow-head directed and moved anteriorly.

**Compound units.** A unit illustrated in Fig. 8 had peculiar properties. It showed quite an active ongoing discharge, but responded neither to diffuse illumination nor to a flashing spot of light. Careful exploration revealed that there were two separate regions sensitive to a moving black target (A and C regions). The black target moving across A region gave rise to an acceleration of spike discharge regardless of the direction of motion. This was also the case with C region. However, similar stimulation given to B region produced an inhibition of ongoing discharge. When the target was moved through A, B and C in this or the reverse order, the spike discharge was first increased, then depressed and again increased as predicted from the characteristics of A, B and C. The contours of excitatory and inhibitory regions were traced by observing responses to the moving target. Two excitatory regions A and C separated by an inhibitory region B were easily demonstrated as shown in Fig. 8. Furthermore, it was shown that excitatory and inhibitory regions were mutually antagonistic. While an accelerated discharge was induced by putting a black target into A region, B region was stimulated by another black target. Covering of B region with the target depressed,
Fig. 8. A compound unit.

Receptive field was composed of three separate regions A, B and C. Only a black target was found to be an effective stimulus. A and C regions were excitatory with respect to the black target, but B region inhibitory. The black target moved across A, B and C in this order or in the reverse elicited responses as shown interaction between inhibitory region B and excitatory regions A and C is shown at the top. The interaction between inhibitory region B and excitatory regions A and C is shown at the bottom. Black right angle corner first covered A region (1). This procedure caused acceleration of discharge. While A region was covered, a small black rectangle covered B region (2) which suppressed the discharge. Then B region was uncovered (3). The discharge was recovered. Subsequently A region was uncovered, the discharge being again suppressed and returning to the initial level. The accelerated discharge and uncovering recovered the discharge and then uncovering of A of region depressed the discharge. All these responses were evoked only by a black target, but not by a luminous spot. The entire receptive field of this unit will be said to consist of three separable subsections which are functionally related.

Depth distribution of units observed

The distribution in cortical depth was examined on 114 units. Fig. 9 shows that no responsive units were observed within 400μ from the cortical surface and that the depth in which units were most frequently encountered was about 1.35 mm or layer V of the cortex. Beyond 2.0 mm most of units were found to be derived from fibers.

Columnar arrangement of cortical neurons

A columnar arrangement of neurons has been first demonstrated in the somatosensory cortex by Mountcastle in the cat\textsuperscript{23} and then by Powell and Mountcastle in the monkey.\textsuperscript{24} In the visual cortex Hubel and Wiesel.\textsuperscript{13,25}
demonstrated the columnar arrangement of cells which had a common property of having the receptive field axis orientation. In the somatosensory cortex neurons involved in a particular column have been shown to be associated with the same modality subgroup and also have peripheral receptive fields which are almost identical. A common factor to identify a particular column is the receptive field axis orientation in the cat’s visual cortex and submodality of sensory stimulus in the somatosensory cortex. As already stated, neurons in the rabbit’s visual cortex differ from those in the cat’s visual cortex in that the receptive field axis orientation is not an essential property in the former. Consequently the receptive field axis orientation is not available for identification of a columnar arrangement of cortical cells in the rabbit. If there are narrow vertical columns of neurons in the rabbit’s visual cortex, what is a common factor to be shared by constituents? To answer this question recordings of as many units as possible were tried in each penetration which was made as perpendicularly to the cortical surface as possible. All units isolated in a penetration were carefully examined for their trigger features.
Fig. 10. Receptive fields of units recorded in a single microelectrode penetration which was made as perpendicularly as possible to the cortical surface.

Main axis of the receptive field is indicated by thick bar. Complex fields are outlined by interrupted lines and simple fields by continuous lines. Depth at which each unit was recorded is shown on the right.

and locations of the receptive fields. Fig. 10 illustrates one of these experiments.

Units 8, 12 and 13 had a well-defined receptive field axis orientation (indicated by thick bar). The most effective stimulus for these units was a moving narrow rectangular light with its long axis oriented in an appropriate direction. The outlines of the receptive fields of these units were unable to be delineated definitely by the flashing spot method. Unit 10 was responsive to a large black edge oriented obliquely when it was moved in the direction perpendicular to its edge. Unit 14 was insensitive to a small spot of light, whether it was moved or stationary, but sensitive to a slit of light regardless of its axis orientation. Units 9, 15 and 17 were of simple ‘on-center’ type. Unit 18 was a fiber unit of an ‘on-center’ type.

This chart shows that (1) neurons involved in a vertical column had receptive field which was almost identical in position (scattering was within a range of 3°), (2) no systematic changes occurred in receptive field organization and characteristics as depth increased, (3) receptive field axis orientation if observed was either perpendicular or parallel to each other, (4) no common factor was detected to specify a column. Furthermore, it was found that directionally selective units recorded in a vertical penetration had not always the same direction to which they were selectively sensitive.
Orientation of long axis of the receptive fields located in the visual streak

In rabbit's retinal ganglion cells of the visual streak Levick showed that their receptive fields had a tendency to be oval-shaped with the long axis horizontal. In the present experiments all the units in the same animal whose receptive field was located in the visual streak were collected and their fields were superimposed with respect to the optic disc and blood vessels running therefrom horizontally together with the white bundle of myelinated nerve fibers. The visual streak is located about 20° below the lower border of the disc, occupying most of the horizontal meridian. Fig. 11 shows the contours of receptive fields of 16 units recorded in the same animal. Most of them were found to be oval-shaped with their long axis almost parallel to the horizontal meridian.

Fig. 11. Receptive fields found in or close to the visual streak. It is to be noted that the orientation of the long axis of the receptive field is parallel to that of large vessels running on the medullary rays. The optic disc is outlined by dotted line together with two large vessels.

DISCUSSION

Properties of cortical neurons studied in the present experiments were not so largely different from those of retinal ganglion cells and lateral geniculate neurons.

Most of cortical neurons in the primary visual area responded to large-field illumination which was turned on and off at about 0.8/sec. Such responsiveness of rabbit’s neurons seems to be in striking contrast to unresponsiveness of cat’s cortical neurons which was reported by Hubel and Wiesel and also confirmed by ourselves.

Another discrepancy to be emphasized between rabbit’s and cat’s cortical neurons is that the axis orientation of the receptive field is not a specific property for rabbit’s neurons as it is for cat’s neurons. According to Hubel and Wiesel, the neurons in the cat’s visual cortex have a specific axis orienta-
tion of the receptive field, and a ‘column’, extending from the cortical surface to
the white matter, is specified by the axis orientation of the receptive field common
to all constituent neurons of the column. In contrast, all cortical neurons of
the rabbit’s visual area had no specific axis orientation of the receptive field as
defined for cat’s neurons. The axis of the receptive field is functionally defined
so that it is coincident with a border between excitatory and inhibitory regions, or
a slit-shaped light stimulus placed in accord with the axis is the most effective to
elicit responses when flashed on and off or moved in the normal direction of the
axis.

These differences could be accounted for by assuming that in the rabbit there is
no rearrangement of neuronal connections between optic nerve fibers and cortical
neurons through geniculate neurons as suggested in the cat by Hubel and Wiesel.\textsuperscript{13}
In other words, neuronal connections in the rabbit’s visual pathway might be
straight forward all the way to cortical neurons. Such a view may be supported
by the findings that neurons in the cortical projection area of the visual streak in
the retina resembled retinal ganglion cells in the visual streak in that the
receptive field was relatively small and oval in shape with its long axis parallel
to the medullary rays. Recently published results of Globus and Scheibel\textsuperscript{26} appear
to be favorable for this view which showed that specific visual projection fibers
synapsed directly on vertically oriented dendrites of cortical pyramids in the
rabbit.

For the rabbit, which is said to be a hunted animal, timid and ready to escape
from predators, such as the cat, early detection of their enemies is vital for surviving.
In this regard the following facts will favor the animal: All of the photoreceptors
in the rabbit’s retina are rod,\textsuperscript{16,17,21} the laterality of the eye position in the head is
so characterized that there is almost no blind area in the visual field with a wide
panoramic uniocular field in sacrifice of binocular field and also the detection of
features of an object is performed already at retinal ganglion cells to consider-
able degree. Incidentally visual acuity of the rabbit is reported to be inferior to
that of the cat which has a wide binocular field.\textsuperscript{28}

According to numerous behavioral experiments\textsuperscript{29–31} the striate area of the
cerebral cortex is essential for detail vision but not for learning light-dark
discrimination. Although we have not met any paper concerning functional
deficits after visual decortication of the rabbit, it could be reasonably inferred that
visual decortication would not lead to a considerable loss of detail vision in this
animal. Behavioral experiments on this matter will be required.

The question asked on starting the present experiments on the role of the
primary visual cortex plays in visual function is not answered definitely on the
basis of the results obtained in these experiments. However, the present
results especially on the compound units will lend a support for the view that some
integrative action on the in-coming visual information is carried out in this
visual center.
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