Functional Characteristics and Diversity of Cat Retinal Ganglion Cells

Basic Characteristics and Quantitative Description

Christina Enroth-Cugell and John G. Robson

Part I
Christina Enroth-Cugell

Basic Characteristics of Ganglion Cell Receptive Fields

Many of you may wonder why anyone would spend the better part of a life-time doing little more than recording from retinal ganglion cells, as I have done, so, I will give some justification for this a little bit later.

Since John Robson has more sense than I, he has done a lot of other things than studied ganglion cells. However, the fact remains that it was John's interest in the behavior of retinal ganglion cells which twenty years ago caused Fergus Campbell to "ship John across the Atlantic" to Northwestern University "to dirty his fingers" with visual neurophysiology. I owe Fergus Campbell much gratitude for having provided me with the opportunity and privilege to work with John, to keep him awake during nightly experiments by giving him frequent feedings and to make life almost intolerable for him by nagging about writing up the results. I hope that I have rendered visual sciences a small service by, in this way, having served as "supportive tissue" for John's brain.

The introductory, very basic, comments on retinal ganglion cell characteristics which follow will, I hope, serve as a necessary background for John's quantitative description of cat ganglion cell behavior and also serve as a tribute to Ragnar Granit and Stephen Kuffler who laid the foundations for our knowledge of, and subsequent approach to, this fascinating subject.

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Reasons for Studying Ganglion Cells

Retinal ganglion cells with their axons provide the sole connecting link between the *receptive* mechanisms of the retina and the more central *analyzing* mechanisms of the visual system. Thus, on the one hand, the signals which travel in the optic nerve are the *outputs* of the complex mechanisms of the retina, while on the other hand, these same signals constitute the *inputs* to the higher visual centers. Since we may suppose that the operation of these central mechanisms (which must ultimately give rise to visual *perception* and *behavior*) may be understood in terms of the further transformations to which signals originating in the retina are subjected, it seems justifiable to try to give an adequate description of the behavior of retinal ganglion cells. But there are also other reasons for studying these cells.

One of these is that the optic nerve forms the weakest link in the visual chain, for there are fewer ganglion cells than there are neurons at any other level of the visual system. It is in the optic nerve that the visual signal is represented most economically and with least redundancy. We may therefore expect that it is at this level that the principles underlying the coding of visual signals will be clearest.

Another reason for choosing to concentrate on the behavior of retinal ganglion cells is that it is in the optic nerve that the flow of information in the visual pathway is most nearly in one direction only. Within both the retina and the higher visual centers there are numerous lateral and feedback circuits which make it harder to make sense of the activity of individual neurons. While the mammalian optic nerve may contain some efferent fibers, there are probably very few (see Itaya 1980).

It is worth mentioning one more reason for studying the characteristics of ganglion cells: convenience. Because, so far as we know, all other mammalian retinal neurons generate only graded potentials, their behavior has to be studied using intracellular recording techniques. Such techniques are really only practicable in

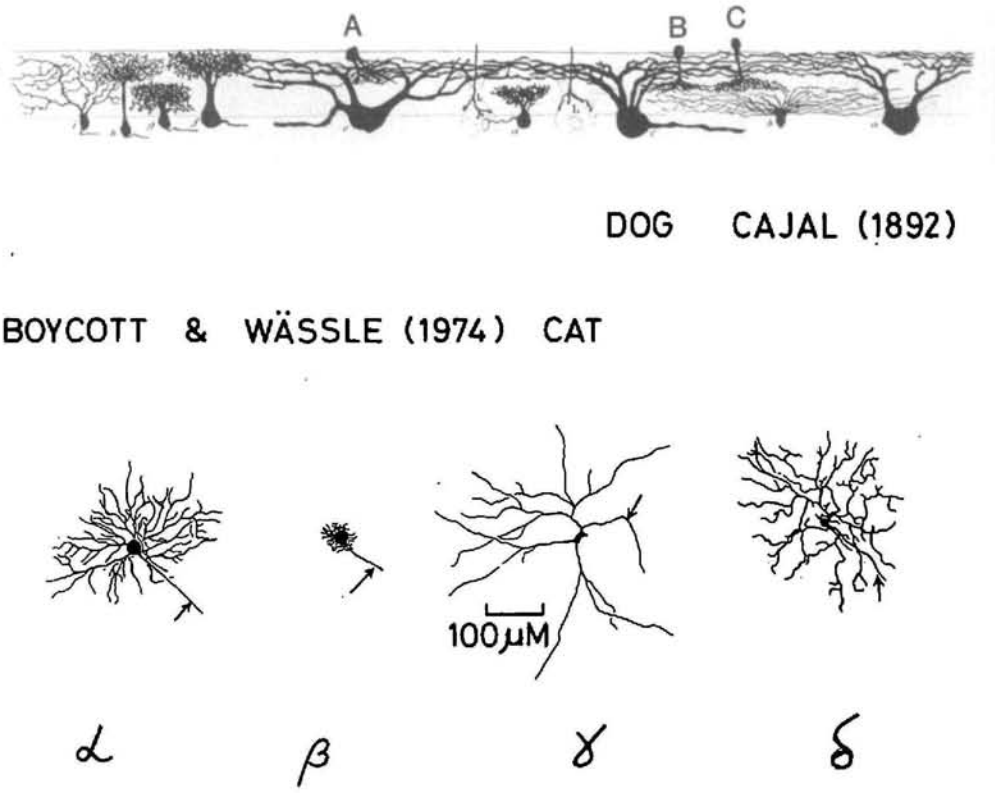

Fig. 1. Retinal ganglion cell morphology. In the lower part the axons of the cells are marked by arrows.

isolated retinal preparations and this effectively limits their routine use to cold-blooded species. Retinal ganglion cells, on the other hand, generate all-or-none action potentials which can be recorded from either the cell bodies or axons with less exacting extracellular methods and this makes recordings in the whole animal a practical proposition. Extra-cellular recording from neurons higher up in the visual system is clearly also possible in whole animals, but the difficulties of interpretation associated with the use of anesthetics and uncertainty about the animal's state of arousal are then more pronounced.

Morphology

While retinal ganglion cells are a well-defined class of neurons, it has been clear for about a century that the ganglion cells of the mammalian retina show a considerable degree of morphological diversity. The upper part of Figure 1 (from Cajal's 1892 monograph) shows a vertical section through the *dog* retina in which all the cells except those labelled A, B, and C are ganglion cells. Without going into details, it will be rather obvious that these ganglion cells represent several different morphological types. In the lower half of Figure 1 are drawings of different types of *cat* retinal ganglion cells as they appear in a retinal flat mount (Boycott & Wässle, 1974). Alpha- and beta-cells constitute two distinct and homogeneous morphological classes while gamma-cells can be distinguished from alpha- and beta-cells but constitute a morphologically *heterogeneous* group within which the delta-cells form a distinct subclass.

Thus, the diversity of retinal ganglion cells described for the dog so long ago has been confirmed in the cat, and, a basis has been laid for the correlation of ganglion cell size and morphology with physiological characteristics. However before turning to the physiology of retinal ganglion cells it is worth making two points. Firstly, although it is well known that there are species differences with regard to ganglion cell morphology these are probably not important in the context of this paper. Secondly, although we shall only be talking about cat retinal ganglion cells, we now have good reason to believe that many of the basic anatomical and physiological principles evident in the *cat* retina also hold for the *primate* retina (see review by Lennie, 1980).

Physiology

All knowledge of the physiological characteristics of ganglion cells had to wait for the development of microelectrodes capable of recording from individual neurons. These were first applied (around 1940) to a study of ganglion cells in the mammalian retina by Ragnar Granit (1947), who was able to demonstrate the importance of both inhibitory as well as excitatory influ-

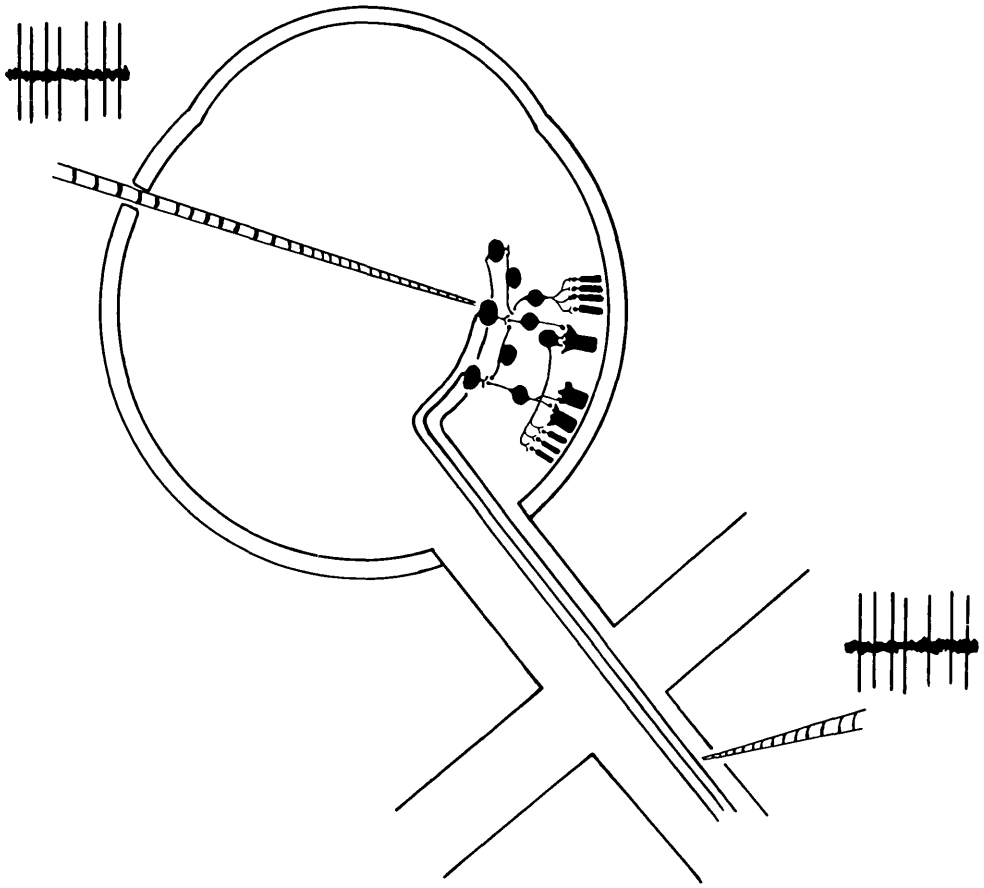

Fig. 2. Schematic representation of action potentials ("spikes") being recorded by an intraocular micro-electrode from a retinal ganglion cell soma and from a ganglion-cell axon by an electrode inserted into the optic tract.

ences in determining the activity of these cells. However our current basic concepts of ganglion cell behavior largely derive from the work of Stephen Kuffler (1952, 1953) who combined the use of microelectrodes for recording directly from ganglion cell bodies in the intact eye of the cat (upper left in Fig. 2) with stimulation of the retina with localized spots of light.

Two of Kuffler's many important findings were, firstly, that the ganglion cells from which he recorded had more or less circular receptive fields organized into concentric antagonistic regions. Secondly, he found ganglion cells of two kinds; they differed in being either excited or inhibited by light falling in the center of their receptive fields. Those that were excited by light, ie, increased their firing rate, Kuffler called ON-center cells; those that were inhibited by light in the center of their receptive fields, ie, decreased their firing rate, Kuffler called OFF-center cells. Although Kuffler described only two types of ganglion cell behavior, it is clear that he anticipated the encounter of other ganglion cell classes, for in 1952 he wrote: "with more refined methods a variety of ganglion cells of different behavior remains to be uncovered." However, subsequent studies were initially directed toward defining more closely the properties of the concentric center-surround cells that Kuffler had described rather than toward searching for cells with different behavior. When John Robson in 1964 came to Northwestern it was with just this aim in mind: we planned to undertake a more quantitative study of Kuffler's ON- and OFF-center cells. More specifically, our intention was to use sinusoidal grating patterns to explore the *physiological* basis for the manner in which the human visual system responds to different spatial frequencies contained in the visual environment. This experimental approach, which reveals particularly clearly the significance of inhibitory processes in the visual system, had recently been introduced by Schade (1956) into the quantitative study of human spatial vision (see also Campbell & Robson, 1968). Our expectation was that the application of similar analytic methods to the study of the properties of retinal ganglion cells would prove particularly satisfactory and convenient, and would contribute useful data to the discussion of the role of the retina in spatial vision. What we had not expected at all was that these experiments would provide any *qualitatively* new insight into retinal ganglion cell behavior. That is, we had not foreseen that we would find that both ON- and OFF-center cells could be subdivided into the two physiologically quite distinct classes to which we gave the noncommittal names X- and Y-cells (Enroth-Cugell & Robson, 1966). That this

finding has in fact prompted some new research into, and thoughts about, the organization of the entire visual system is to be credited exclusively to our colleagues in different parts of the world.

The essence of the spatial frequency approach to the study of vision and visual neurons is the adoption of a particular stimulus, the sinusoidal grating, and this will be discussed in detail later. However, what I want to do now is to recall some of the things about ganglion cells that can easily be demonstrated using the intuitively more appealing form of visual stimulation used by Kuffler, ie, stimulation by spots of light of various sizes located in different places within the receptive field.

First let me point out two ways in which the activity of an individual ganglion cell can be recorded with a micro-electrode. As schematically represented in Figure 2, this can be done either directly from the soma of the cell with an electrode which is inserted into the eye through a small hole in the sclera just behind the ciliary body, or alternatively it is possible to record from the axon of the cell as it runs in the optic tract towards its central destination. Whichever recording site is chosen, ganglion cell activity is manifest as a succession of action potentials or "spikes." These trains of spikes which constitute the only signals leaving the eye, occur more or less irregularly at average rates which are commonly something like 20–60 per second. This ongoing or maintained activity is seen in most retinal ganglion cells even when the cat is looking at a uniformly and steadily illuminated field, or is left in complete darkness, and there is no specific visual stimulus. The maintained activity provides a baseline level against which both increments and decrements can be signalled, as we shall see in the next two figures.

The first of these (Fig. 3) illustrates the behavior of an ON-center cell. The row of squares at the top of the figure indicates that during the approximately 2 seconds that the figure spans (from left to right) the cat looks at an oscilloscope screen larger than the cell's receptive field. The outer circles in the squares roughly outline the limit of the receptive field surround while the smaller circles show the approximate limit of the receptive field center. Over to the left (square 1) the uniform grey means that at first the cat faces nothing but a steady uniform background which causes the cell to fire spikes at a maintained rate of just under 50 impulses/second (trace C). When the illumination of a part of the center is temporarily increased above the background level (square 2) the cell responds with an increase in its firing rate. This is just barely detectable in the two spike trains (B) although in C, which is a firing-rate record obtained by averaging over many cycles of the stimulus, it is very obvious that increasing the center illumination and hence introducing a *positive* contrast between center and surround, causes the cell to respond with an increased firing rate. Conversely, when the spatial contrast becomes *negative* (ie, the center is made darker than the surround as in square 4) the result is a decrease in firing rate. Whether a spatially localized stimulus increases or decreases the firing rate of the cell, the effect is maximal a few tens of milliseconds after the onset of the stimulus. Thereafter the cell's firing rate drifts back towards its prestimulus level, initially rather quickly but subsequently more and more slowly. Characteristically also, when a stimulus is removed after having been present for some time (as in Fig. 3), the cell's firing rate is transiently changed in a sense *opposite* to that resulting from the onset of the stimulus.

ON- and OFF-center cells respond in opposite ways. For an OFF-center cell to respond with an increase in firing rate the illumination at the center of its receptive field has to be decreased relative to the surrounding area, while increasing the illumination at the center decreases the firing rate.

The firing rate of a ganglion cell can most easily be changed by a *small* stimulus if this falls in the very middle of the cell's receptive field (as in Fig. 3) because that is where the sensitivity is at a maximum. But changing the illumination relative to the center over a large part of the less-sensitive surround can be equally (or even more) effective. This is illustrated for an OFF-center cell in Figure 4. Again, this figure suggests that the cat first faces a uniformly illuminated oscilloscope screen. Then (square 2) the whole receptive field center is suddenly dimmed for about 200 milliseconds resulting in an abrupt *increase* in firing frequency because we are here dealing with an OFF-center cell. After a second period (square 3) of the same uniform illumination as initially, the light within the *center* of the receptive field is kept constant while the luminance of the rest of the oscilloscope screen, and hence the illumination of the receptive field surround, is reduced (square 4). Now the cell abruptly decreases its firing rate so long as the stimulus lasts and the time-course of the decrease is very similar to that of the earlier increase.

Another very important feature of retinal ganglion cell behavior is illustrated over to the right in Figure 4. After the cat has looked for a while at the oscilloscope screen illuminated uniformly at the original level (square 5) the entire screen is dimmed. That is, this time the light level changes simultaneously over the center and the surround, by the same amount, and in the same direction. To this kind of stimulus the cell responds (below square 6) with nothing but a small and short-lasting increase in firing rate as the screen illumination is suddenly lowered and with an equally short-lasting small dip in firing rate as the illumination

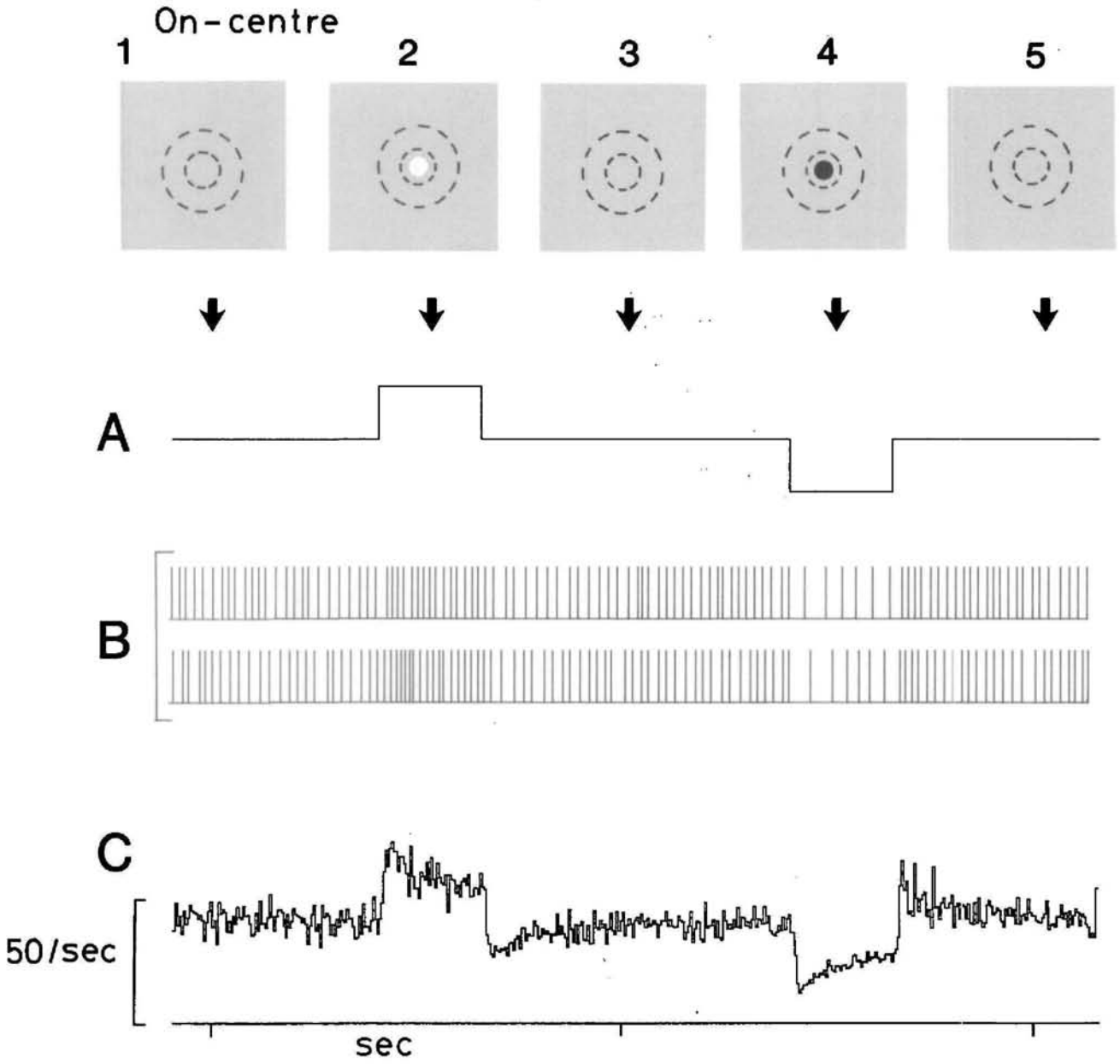

Fig. 3. A model ON-center cell responding (A) to changes in illumination within its receptive-field center. The spike trains in B (and also those shown in Figs. 4, 6, and 7) are computer-generated (not actual ganglion-cell recordings) but realistically mimic retinal X-cell behavior. The trace in C shows the cell's firing rate as a function of time and is generated by averaging over many repeated responses. More details in text.

simultaneously returns to its original level over both the center and the surround of the cell's receptive field (square 7).

To summarize the two points made by Figure 4: firstly, equal and opposite effects on a ganglion cell's firing rate can be produced by independent stimulation of the center and surround of its receptive field. Secondly, although the sensitivities of the center and of the surround are differently distributed spatially, their total *integrated* sensitivities are usually so balanced that if the illumination over the entire center and over the entire surround are changed in the same direction and to the same extent, then there is only a small transient effect on the cell's firing rate. In this way ganglion cells are rendered relatively insensitive to changes in stimulus luminance as such, while remaining particularly responsive to changes in spatial contrast. Ganglion cells will respond best to spatial patterns which cause the receptive field center to be illuminated at one level while the surround is illuminated at a different level. This means that when a ganglion cell is stimulated with a grating pattern it will

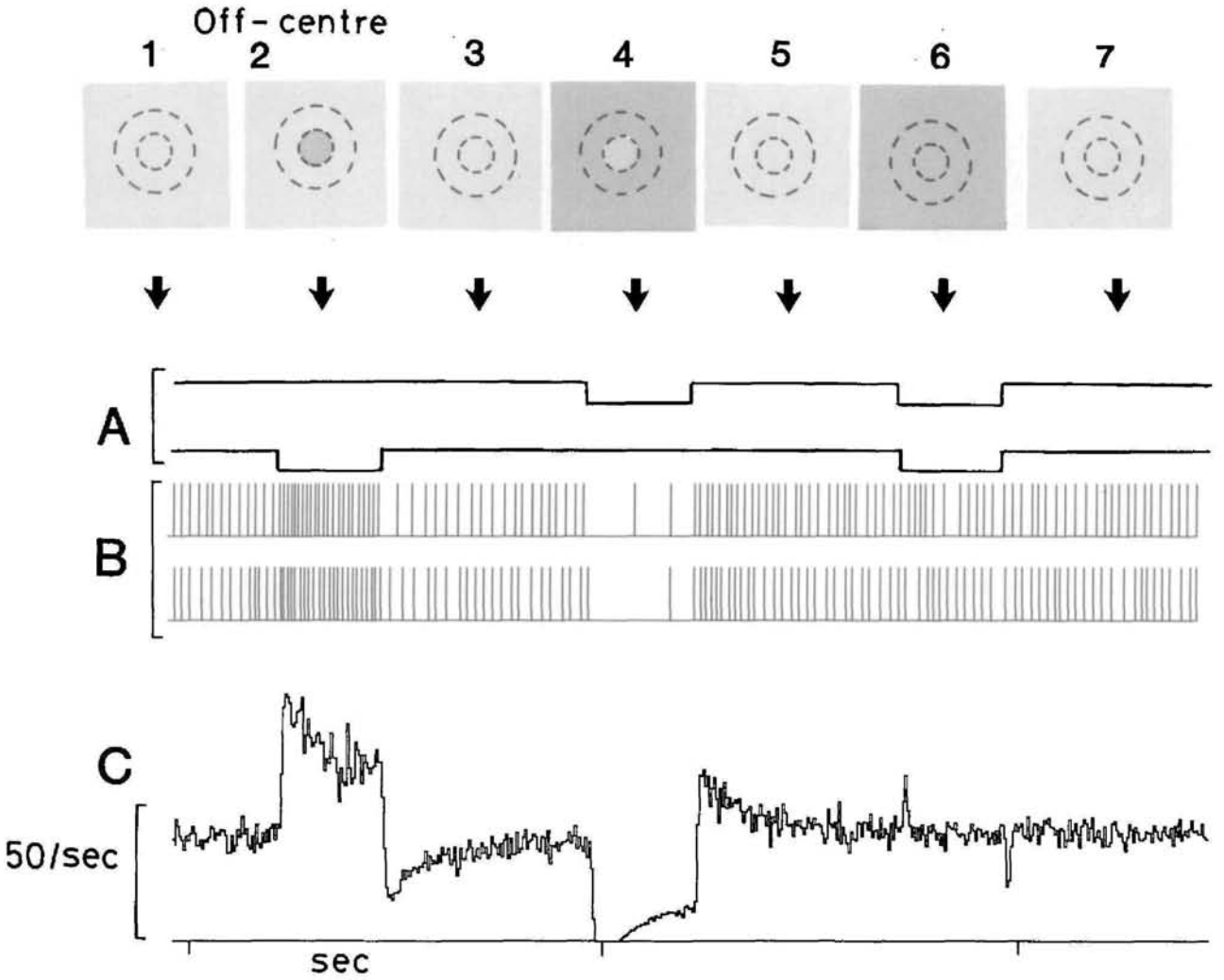

Fig. 4. A model OFF-center cell responding to decreasing illumination in the center of its receptive-field (2), in the surround of its receptive-field (4) and over its whole receptive field (6). Detailed description in text.

respond especially well at certain spatial frequencies or in other words it will demonstrate spatial frequency tuning.

The fact that the response of a ganglion cell is a modulation of the rate of a pre-existing discharge has several implications. Firstly it makes it possible for the occurrence and strength of weak stimuli to be signalled more readily. If ganglion cells had no ongoing discharge in the absence of specific stimulation, then it would be necessary for the strength of a stimulus to exceed some threshold level before any spikes could be fired at all. Secondly if, as we believe, the strength of a stimulus is indicated by the rate at which the cell fires, then, in the absence of an ongoing discharge, the strength of a weak stimulus could only be indicated after a considerable delay, since the rate of firing cannot be determined until at least two spikes have been generated (and at a low rate this would be a long time). By having a maintained discharge whose rate is simply altered by the stimulus, it is in principle possible to signal the occurrence and strength of a weak stimulus in a time roughly equal to that between successive spikes in the ongoing discharge. Moreover there is in this case no reason why indefinitely weak stimuli should not produce changes in the spike discharge rate (as they seem to), although these changes may be so slight as to be difficult to detect subsequently.

Although there may be no problem in transmitting information about weak stimuli in a system of this kind, there is a potential problem with strong stimuli. While information about a stimulus which *increases* the firing rate of a ganglion cell may, within limits, be adequately signalled by the cell's increased firing rate, a strong stimulus which *decreases* the rate may either stop the discharge altogether (in which case no detailed information will be available at all), or, if rather less

strong, may slow it down enough to make information about the reduced firing rate available only after some long time. It is plausible that both ON- and OFF-center ganglion cells have evolved so that information about strong stimuli will always be adequately signalled by an increase in the discharge rate of some cells.

Part II
John G. Robson

Quantitative Description of Retinal Ganglion Cell Behavior

What I want to do is to discuss *how* one can obtain, and also a little about *why* one might want to obtain, a quantitative description of retinal ganglion cell behavior.

What do we gain from having quantitative information about ganglion cells? Firstly, a quantitative description may be useful simply because numbers and mathematical formulations can have more precise meanings than verbal description. Thus, by providing a quantitative description it is possible for one investigator to convey his or her findings and interpretation of ganglion cell characteristics to another investigator more exactly and with less ambiguity and chance of misunderstanding than when reliance is placed solely on imprecise subjective or qualitative information. This may well be of consequence, for example, in generating a scheme of cell classification, even when the particular numbers or mathematical formulation have no other special significance.

Secondly, since one of the reasons for studying ganglion cells in the first place is to determine what role they play in the visual process and to what extent the nature or limitations of visual performance are dependent upon retinal function, it is desirable to characterise the behavior of ganglion cells in such a way as to make it possible to predict how a cell will respond to many different stimuli. If this is to be done without exhaustively testing cells with each different stimulus of interest, it is necessary to generate a "model" of the cell's behavior which will allow the response to an arbitrary stimulus to be predicted. Even if one is only interested in a *qualitative* prediction of the form of a cell's response this will still in general only be possible if a *quantitative* model is formulated.

Thirdly, one may simply adopt the view that if ganglion cell behavior is amenable to quantitative analysis, as it surely must be, then a purely qualitative description is incomplete, and one cannot claim to have a full understanding of ganglion cell behavior without it.

Anyway, let us suppose that for one of these reasons we decide to derive a model of ganglion cell behavior. How do we set about it?

Receptive Field Models

It is natural to assume from the general description of the antagonistic center/surround organization of the ganglion cell's receptive field that the first thing we should do is to find out how the cell's responsiveness varies over the extent of its receptive field. For if it is the case, as has been implied (eg, Rodieck, 1965), that the response of a ganglion cell is the sum of the responses to stimuli in different parts of its receptive field, then we might expect to be able to predict the response to an arbitrary stimulus pattern if we knew what the response of the cell would be to each of the little elements, spots if you like, of which the stimulus can be imagined to be composed. We might then consider it appropriate to measure the responsiveness of a ganglion cell at different points in its receptive field by recording the responses to light or dark spots placed at these different points. While this is all very fine in principle, in practice there are problems. Let us look at Figure 3 again. Here we see the response of one of the commonest type of cat ganglion cells (an X-cell) to a not-so-small spot placed in the most sensitive (most responsive) region of its receptive field (ie, at the very middle of the receptive field). Even with this stimulus the response is sufficiently small, in comparison with the variability of the ongoing discharge, to make it necessary to average the responses to quite a large number of presentations of the stimulus before we can get a good measure of the waveform, or even just the amplitude, of the response (compare B with C in Fig. 3). If we are to make measurements at a large number of positions in all of which the sensitivity will be less than at the very center, then we find that it takes an impossibly long time to obtain a full set of accurate measurements. This is especially true if we make the spot smaller than in Figure 3 so as to make the interpretation of the measurements more straightforward. Moreover, we cannot save time by measuring in selected locations only. For unless we know how the sensitivity varies over the whole receptive field, we cannot predict how any stimulus which itself covers the whole field will affect the cell.

Why Sinusoidal Gratings?

There are many possible sets of stimuli other than a large array of spots which we could use to derive our model. One set is particularly attractive: this is a

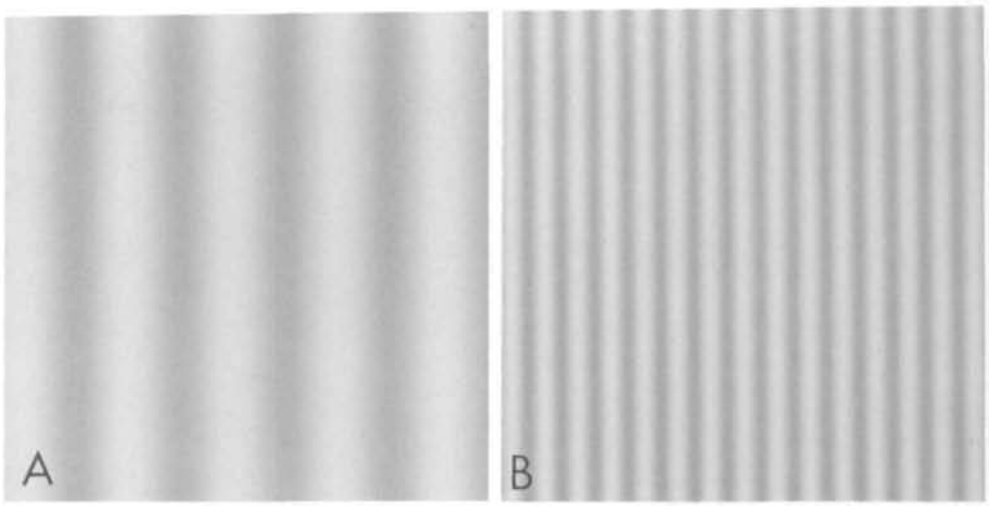

Fig. 5. Sinusoidal gratings generated on the screen of a cathode-ray tube to be used as visual stimuli. The *spatial frequency* of the grating on the right is higher than that on the left.

set of sine-wave gratings of different spatial frequencies. Figure 5 shows a sine-wave grating of low spatial frequency and another of higher spatial frequency.

One reason for using sine-wave gratings as stimuli is that any arbitrary stimulus pattern can just as well be considered as the sum of a whole lot of independent sine-wave gratings of various spatial frequencies, orientations and contrasts (Fourier synthesis: eg, see Weisstein, 1980), as it can be thought of as being made up of a whole lot of independent little dots of various luminances, and the mathematics of sine-waves are often easier to handle than the mathematics of dots. A second reason for choosing sine-wave gratings as stimuli is that sine-wave gratings are "eigen functions" for any linear imaging system. This means that the "image" of a sine-wave grating formed by any system which operates linearly is itself always a sine-wave grating. Thus to the extent that the neural mechanism of the visual system behaves linearly (the optics of the eye certainly behaves as a linear imaging system) we know in advance what the spatial distribution of the neural responses will be if we use a sine-wave grating as a stimulus. This would not be true for any other periodic stimulus pattern. A third reason for using sine-wave gratings as test patterns is that they lend themselves very well to the analysis of responses to stimulus motion. This is because the lateral movement of a sine-wave grating gives rise to a temporal sine-wave modulation of the luminance which at every point in the image is of the same frequency and amplitude, though the temporal phase of the modulation will vary from point to point. Fourthly, sine-wave gratings (unlike small spots) are good for studying retinal ganglion cells because they are also demonstrably good stimuli for neurons in the visual cortex. This is not only because they are linear stimuli, in the sense that they are composed of parallel lines of different luminances, but also because many cortical cells appear to be particularly sharply tuned in the domain of spatial frequency. A fifth useful characteristic of sine-wave gratings is that spatial frequency, contrast and orientation can all be varied without affecting the state of light adaptation of the cell's receptive field; level of adaptation is set by the mean luminance of the grating.

And lastly we may consider it opportune to characterise the behavior of ganglion cells and indeed other visual *neurons* as well, using stimuli of a kind which have proved useful for characterising *human* vision. It was for this last reason, in fact, that as a callow youth I set sail (or rather I suppose took wings) to the New World in 1964 to try, with the benefit of Christina's experience of recording from cat retinal ganglion cells, to find out how these cells would respond to the new-fangled sine-wave gratings whose visual detectability Fergus Campbell and I (Robson and Campbell 1964) had been studying back in Cambridge (England). But before we get to describing just how we use sine-wave gratings as stimuli, I think it may be helpful to consider briefly another use of sine-waves, this time as the waveform of the *temporal* modulation of a stimulus. The use of temporal sine-waves as test inputs for the study of the dynamics of physical systems has a long history, and the particular use of *spatial* sinusoidal stimuli (sine-wave gratings) I am going to emphasize here is one in which the *temporal* modulation of the stimulus is also sinusoidal. When working with retinal ganglion cells it is, of course, always necessary to introduce some temporal modulation of the stimulus in order to be able to distinguish the cell's *response* from its maintained discharge.

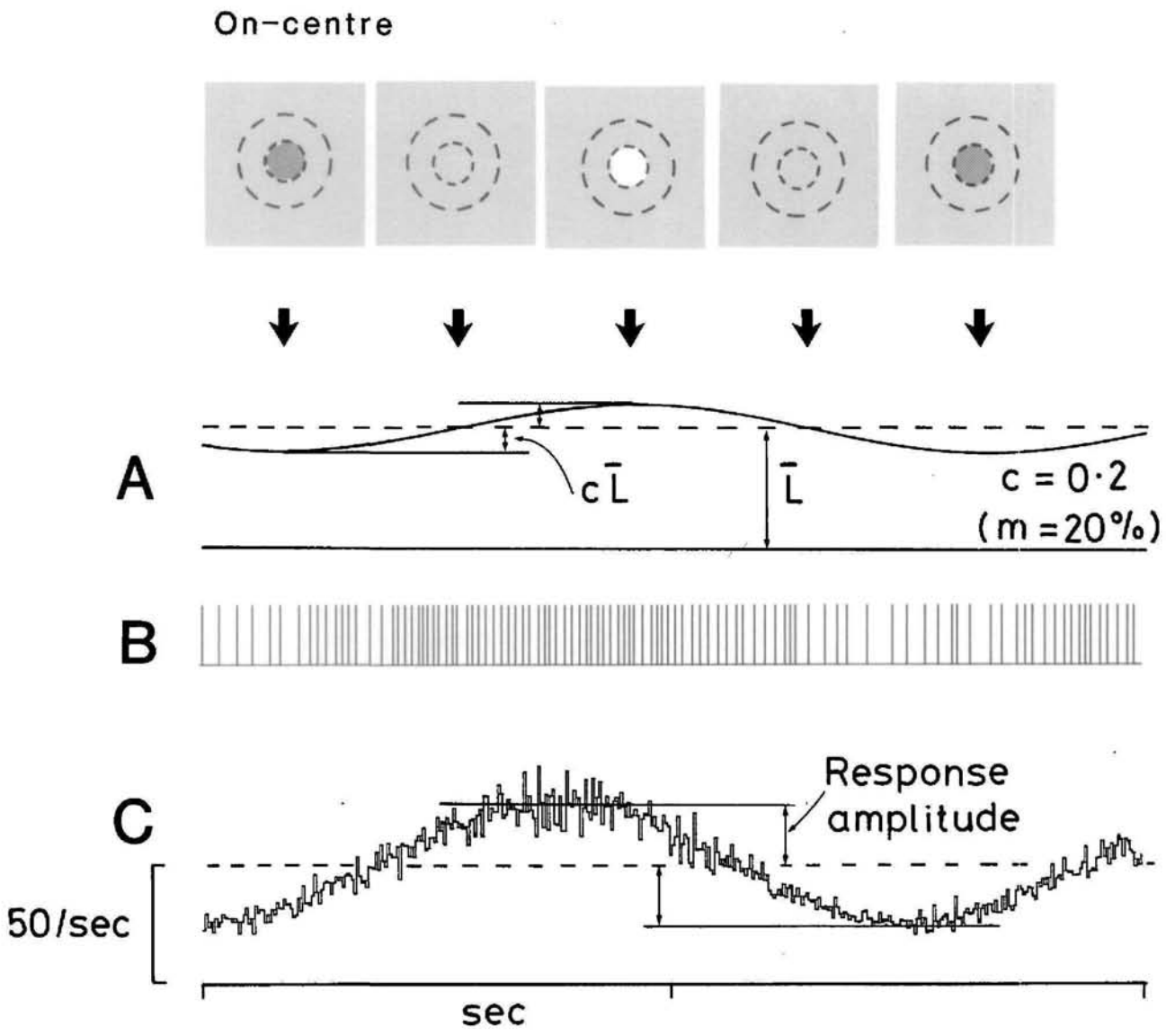

Fig. 6. A model ON-center cell responding to the *temporal* sinusoidal modulation of a spot in the center of its receptive field. See text.

Temporal Sinusoidal Stimulation

The stimuli we shall ultimately get round to discussing are modulated sinusoidally in both time as well as space. But as a link with the behavior of ganglion cells in response to small flashing spots, as illustrated in Figures 3 and 4, let us look at Figure 6 which shows the response of an X-cell to a small spot modulated sinusoidally in time. The spot is centered in the middle of the receptive field. The squares at the top are snapshots of the stimulus at various instants in the cycle during which the luminance of the spot varies sinusoidally above and below some mean level, which in this case corresponds to the unchanging steady level of the background. The sinusoidal variation of luminance at the center of the receptive field is shown as the uppermost trace (A) in which the stimulus amplitude ($c\bar{L}$) and the mean level ($\bar{L}$) are also indicated. We define the modulation depth of this stimulus as the amplitude of the sine-wave variation divided by the mean level. The modulation depth of the central spot in this example is 20% and, since the mean luminance of the spot is equal to the steady background level, the spatial contrast is also varying between + and −20% (ie, between + and −0.2) during the cycle. This kind of stimulus can be called a sinusoidal *contrast-reversing* stimulus.

Examples of the discharge of this ideal center/surround ganglion cell are shown in the next trace (B) while at the bottom (C) we have a representation of the average firing rate of the cell. The periodic variation in the discharge rate of the cell is obvious in trace B,

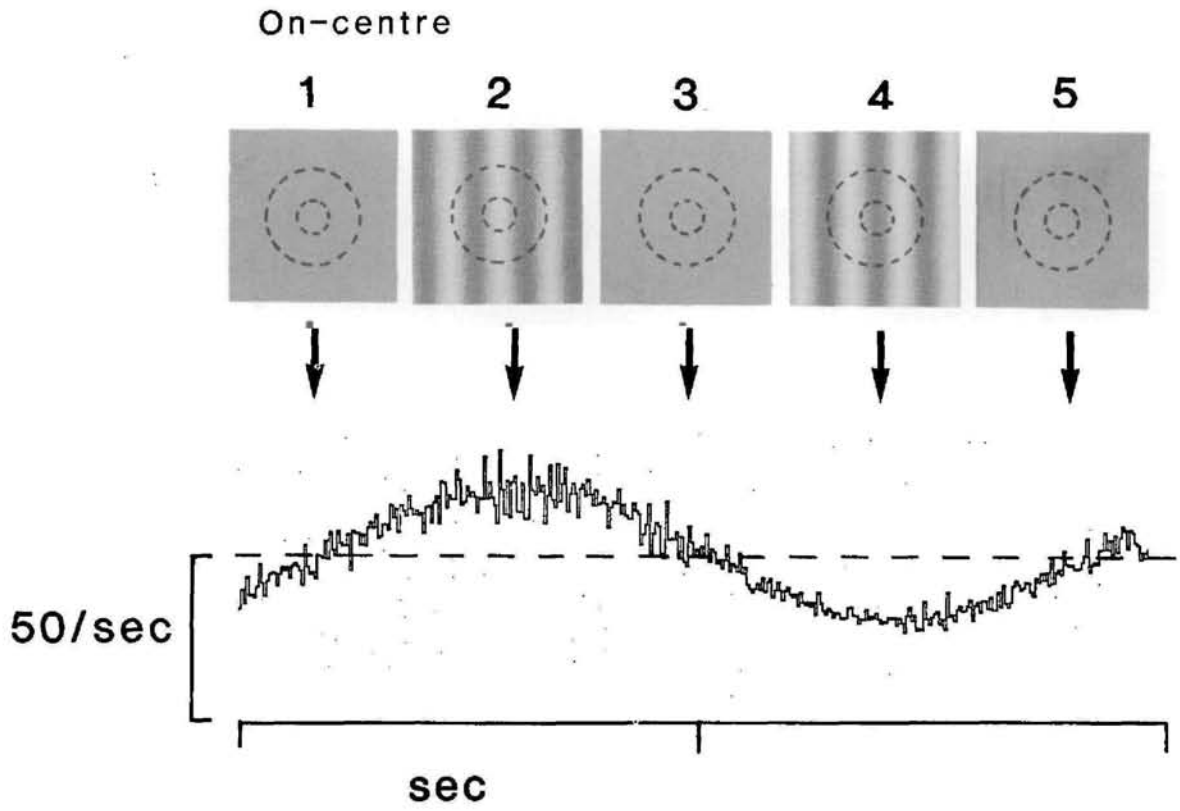

Fig. 7. A model ON-center cell responding to a sinusoidally contrast-reversing sine-wave grating of optimal spatial frequency positioned, relative to the cell's receptive field, to elicit a maximal response. See text for further details.

though we need to examine a firing-rate record of the kind shown in C to appreciate the actual waveform of the variation throughout the stimulus cycle.

You should note three things about the responses of ganglion cells to such sinusoidally contrast-reversing stimuli. Firstly, many cells stimulated in this way actually do generate as a response a sinusoidal, or very nearly sinusoidal, variation in firing rate. This is of interest because it is a characteristic of all linear dynamical systems that they respond to a sinusoidal input with a sinusoidal output. Non-linear devices, on the other hand, can generally be expected to give a non-sinusoidal response and it is often appropriate to gauge the extent of the non-linearity by the magnitude of the deviation of the response from a perfect sine-wave. Secondly, if we get a sinusoidal variation in firing rate we can use the amplitude of this sinusoid as a measure of the strength of the response. While this could be measured directly from a firing-rate record, as indicated in Fig. 6C, it is much better done by performing a Fourier analysis of the response (ie, analysing the response into sinusoidal components) and then measuring the amplitude of that component which is at exactly the frequency of the stimulus (the first harmonic or fundamental component). This produces a considerable improvement in the signal-to-noise ratio of the measurement which is very useful in circumstances such as this where the irregularity of the ongoing discharge is a seriously limiting factor in making precise response measurements. But using the first harmonic as a response measure also allows useful measurements to be made even when the response is not exactly sinusoidal. Fourier analysis can also be used to measure the amplitude of the harmonic distortion components in the response (components at exact multiples of the fundamental stimulus frequency) and thus provide a quantitative measure of non-linearity (see Figs. 8 and 13). Thirdly, we should note that complete characterisation of the response at *one* frequency requires us to measure not only the amplitude of the response but also its phase (or time delay) relative to the stimulus, while complete characterisation of a neuron's behavior requires measurements of amplitude and phase over the full range of temporal frequencies. While the dynamics of ganglion cell behavior is an important topic in its own right, we do not have time to consider it in any detail here and I will only point out that if you are deliberately seeking not to become too involved in temporal aspects of ganglion cell behavior there is much to be said for using stimuli that are sinusoidal in time. This is because, in the ideal case at least, the form of the response (which will be sinusoidal) will be

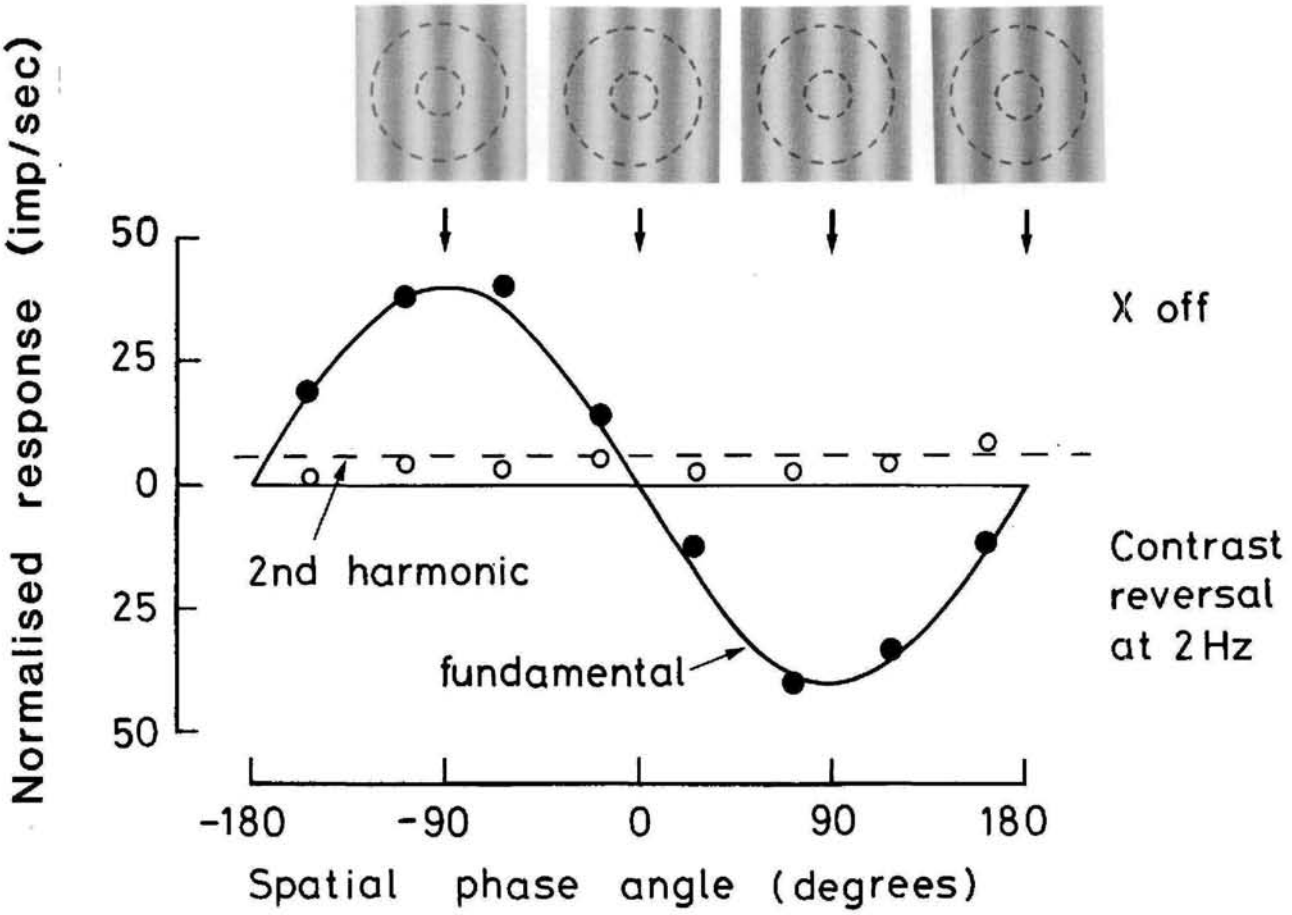

Fig. 8. Experimental results from a cat retinal OFF-center X-cell showing that the amplitude of the fundamental component of the cell's response to a sinusoidally contrast-reversing sine-wave grating (filled symbols) varies sinusoidally as a function of the spatial phase (ie, the position) of the grating. The points representing responses obtained with spatial phase angles between 0 and 180 degrees have been plotted downward to make it easier to see the sinusoidal form of this relationship and in recognition of the fact that the temporal phase of these responses is opposite to those obtained with spatial phases of 0 to −180 degrees. Note that the response is greatest when the spatial phase is −90 or +90 degrees, that is when the grating lies with even symmetry over the center of the receptive field, and zero when the spatial phase is −180, 0 or 180 degrees, that is when the grating lies with odd symmetry over the receptive field (see pictures at the top of the figure).

independent of the spatial configuration of the stimulus. We have already seen that this is not the case when we use on-off stimulation (Fig. 4).

Now at Last to Gratings

Let us suppose we generate a sine-wave grating pattern on a TV type of display. It is then an easy matter to make the contrast of this pattern change sinusoidally in time. The pictures at the top of Figure 7 show how such a stimulus looks at various instants during one cycle of temporal modulation of the contrast. Twice in each cycle the stimulus is a uniform field while between these times the contrast builds up to a maximum before subsiding to zero again. In each successive half cycle the spatial phase of the pattern will reverse so that dark and light bars are interchanged. If we position such a contrast-reversing grating with respect to the receptive field of a center-surround ganglion cell as shown in Figure 7 with either a light bar (square 2) or a dark bar (square 4) lying squarely across the receptive field center then the luminance at the center of the receptive field will vary sinusoidally in time about its mean level pretty much as though we had a sinusoidally modulated spot in the center of the field. As we saw in Figure 6 this gives rise to a sinusoidal modulation of the cell's discharge rate. In this example (Fig. 7) where the width of one bar in the grating approximately equals the diameter of the center there will be some additional components of the response coming from the receptive field surround since this is being subjected to net stimulation in antiphase relative to the center, largely by the half periods of the grating adjacent to that covering the center. That is, the spatial frequency chosen in this example is roughly optimal for this particular cell. The overall effectiveness of the stimulus can be determined by measuring the amplitude of the response. Assuming we consider just one temporal frequency, the amplitude of the response to this stimulus can be expected to depend upon three things: (1) the position of the grating relative to the middle of the receptive field (ie, spatial phase of the

grating), (2) the contrast of the grating and (3) its spatial frequency.

If the ganglion cell behaves linearly the first two of these relationships are predictable: the response amplitude should be (1) proportional to the contrast of the stimulus and (2) a sinusoidal function of its spatial phase. An example of how well the second relationship obtains in practice can be seen in Figure 8 in which the filled and open circles are experimental data from an actual cat experiment (not computer generated). In Figure 8 the amplitude of the response to contrast-reversing gratings is plotted as a function of the spatial phase of the grating relative to the midpoint of the cell's receptive field. Again, the squares at the top represent the stimulus at those instants in time at which its contrast is at a maximum. The −90 and +90 degree positions correspond to the optimal positions of the grating shown in Figure 7. In these positions the grating lies with even symmetry across the receptive field and the temporal variation of luminance at the very center of the receptive field is greatest. The response is at a minimum when the spatial phase is −180, 0 and +180 degrees, the positions at which the grating lies with odd symmetry across the receptive field and the luminance at the midpoint of the receptive field center remains constant at the mean level through the entire temporal cycle. In these latter positions any change in luminance over one half of the receptive field is accompanied by an equal but opposite change over the other half and it is not really surprising that the net effect is zero. In between these cardinal positions the amplitude of the response follows the predicted sinusoidal variation with spatial phase. I should perhaps emphasize that this result is typical of the behavior of a large majority of the cells which can be recorded with an intraocular microelectrode. It serves as one of the indications that these cells behave more or less linearly.

Another indication of the linear behavior of these cells is the low amplitude of the second harmonic component of the response which is indicated in Figure 8 by the open circles and dashed line. This component is the principal distortion component present in the response and in fact it barely rises above the noise level of the measurement.

Yet another finding that is concordant with the approximately linear operation of these cells is that the amplitude of their response (the fundamental) to a contrast-reversing grating in its optimum position is proportional to pattern contrast at least for levels of contrast and response which are not too large. This proportionality between response amplitude and stimulus contrast makes it appropriate to normalise any response-amplitude measurements that we make by dividing the amplitude of the response by the contrast of the stimulus that was used. This then means we don't need to specify the stimulus contrast that was in fact employed. The vertical scale in Figure 8 is marked in this way.

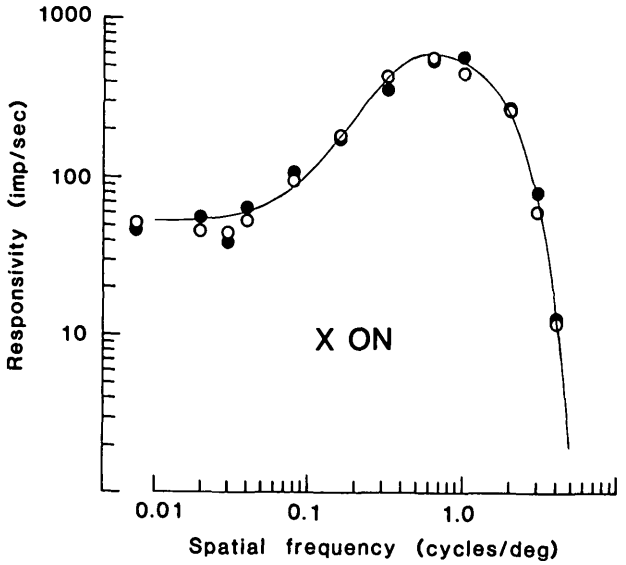

Fig. 9. The spatial-frequency responsivity function of a cat retinal ON-center X-cell measured at 2 Hz. The filled symbols represent measurements made with sinusoidally contrast-reversing gratings fixed in the optimum position while the open symbols represent measurements made with drifting gratings (from Enroth-Cugell, Robson, Schweitzer-Tong & Watson 1983).

Since the amplitude of the fundamental component of the response of a ganglion cell to a contrast-reversing sine-wave grating of any spatial frequency is predictably and demonstrably a sinusoidal function of the grating's spatial phase, we can characterize the responsiveness of the cell to gratings of a given spatial frequency by measuring only the response amplitude for the optimum spatial phase.

When we make such measurements with sine-wave gratings of various spatial frequencies and contrast reversing at 2 Hz, we consistently get results of the kind shown in Figure 9. There we have plotted the normalised response, the "responsivity," of a typical ganglion cell showing linear behavior as a function of spatial frequency. Both responsivity and spatial frequency scales are logarithmic. It is clear that the responsivity of this ganglion cell is markedly dependent upon the spatial frequency showing a clear maximum at some intermediate spatial frequency, a rapid and complete attenuation at higher spatial frequencies and a less complete and rather less abrupt fall-off at lower spatial frequencies. The bandpass form of this function, which we may call a *spatial frequency responsivity function,* is typical of all linearly-behaving ganglion cells.

The Difference of Two Gaussians

For many purposes it is convenient to have a simple mathematical formulation which describes the shape

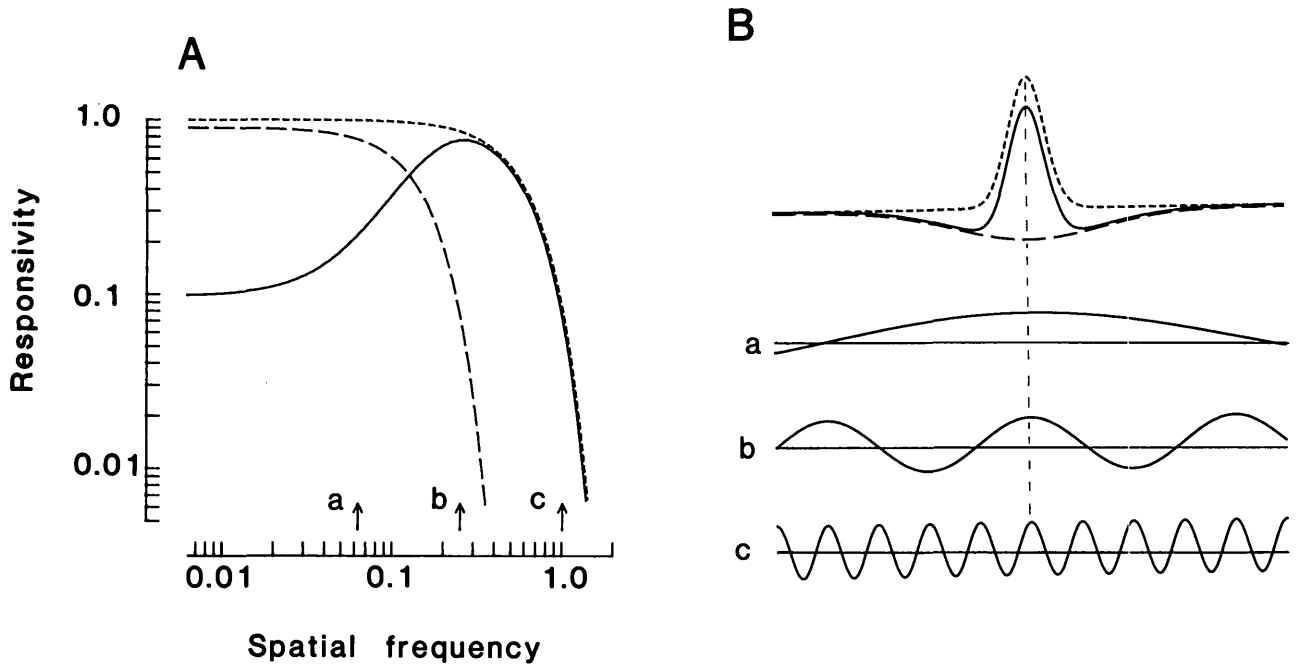

Fig. 10. Modelling the ganglion-cell spatial-frequency responsivity function and receptive field weighting function as the difference of two Gaussian functions. In A the full line represents the spatial-frequency responsivity function of a typical linear retinal ganglion cell (cf, the experimental results of Figure 9 which are fitted with a function of this kind). This curve is the difference between two component Gaussian functions which are shown by the broken lines. These component functions may be related to separate antagonistic mechanisms which have spatial-frequency responsivity functions of nearly the same zero-frequency magnitude but cut-off frequencies which are different. In this example the ratio of the zero-frequency responsivities of these mechanisms is 0.9 while their cut-off frequencies are in a ratio of 1:4. In B the full line in the top sketch represents the spatial distribution of responsivity to a narrow line which would give rise to the spatial-frequency responsivity curve of A. Fourier theory shows that the full curve in B must also be the difference of two Gaussian functions and these components are also indicated by broken lines (for convenience the broader curve is drawn downward so that the resultant function, the full line, appears as the sum of components of opposite sign rather than as difference between component functions of the same sign).

Examination of the top sketch in B suggests that the component mechanisms can be appropriately identified as the receptive-field center (shorter dashes) and a concentric receptive field surround (longer dashes). The narrower center mechanism responds to higher spatial frequencies (line with shorter dashes in A) than the wider surround mechanism (longer dashes in A). The near equality of the zero-frequency responsivities of the center and surround mechanisms evident in A is reflected in the near equality of the areas under the spatial weighting functions of these mechanisms in B. Some intuitive feeling for the relationship between spatial weighting functions and spatial-frequency response may be obtained by considering how well the mechanisms whose line weighting functions are shown in B would respond to the gratings of various spatial frequencies whose luminance profiles are also shown in B. These gratings are placed in the optimal positions with respect to the midpoint of the receptive field and their frequencies are indicated in A (note that the frequency scale in A is marked in terms of the number of cycles of the grating which extend across the center mechanism between the points at which its responsivity has fallen on each side to 1/e of the maximum.)

of the spatial frequency responsivity function. It is nearly always possible to fit the experimental data with a curve which is the difference of two Gaussian functions of spatial frequency. The full line in Figure 9 is such a function while the dashed lines in Figure 10A show the two component Gaussians of which the solid curve is the difference. The right-hand one of these component curves forms the high frequency descending limb of the overall function while at the lower spatial frequencies the overall function represents the fairly small difference between the two component curves in the region in which they approach their low frequency asymptote levels. These two component Gaussian curves can be interpreted as being respectively the spatial frequency responsivity functions of the antagonistic center and surround mechanisms of the ganglion cell's receptive field. That is, the right-hand Gaussian predicts how the *center mechanism alone* would respond to gratings of various spatial frequencies, while the left-hand Gaussian predicts how the *surround alone* would respond assuming that its response could somehow be isolated from that of the center.

The central mechanism, because it has a smaller spatial extent than the surround mechanism, responds to higher spatial frequencies than the surround (see Fig. 10A and B and its legend). Indeed at spatial frequencies above the overall optimum, the response of the cell may be supposed to reflect that of the center mechanism alone. At low spatial frequencies the component curve of the surround indicates that its responsivity becomes significant and the low overall responsivity reflects the antagonism between center and surround. Typically, as in Figures 9 and 10, the surround is a little bit less responsive than the center at the very low spatial frequencies and the cancellation

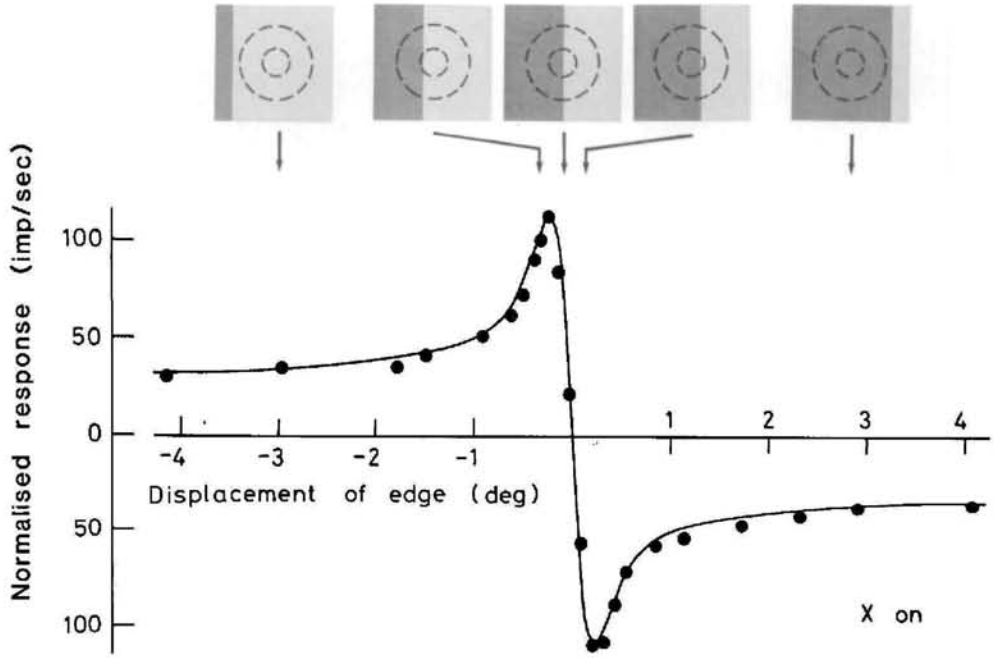

Fig. 11. The response amplitude of a cat retinal ON-center X-cell stimulated by a sinusoidally contrast-reversing edge as a function of the distance of the edge from the mid-point of the cell's receptive field. The contrast of the stimulus was always small enough for the amplitude of the fundamental component of the response at 2 Hz to be proportional to the contrast. The measured amplitude of response was normalised by dividing by the contrast of the stimulus actually used.

is not quite complete even down at zero spatial frequency (ie, when the stimulus has no spatial contrast at all, only a temporal modulation).

Predicting How a Retinal Ganglion Cell Responds to Stimuli Other than Sinusoidal Gratings

As pointed out above, one of the benefits of obtaining quantitative information about ganglion cells is that one can generate a "model" which will allow the cell's response to an arbitrary stimulus to be predicted. By fitting difference-of-Gaussian functions to spatial frequency responsivity data for a ganglion cell (as in Fig. 9) one can get good estimates of the cut-off frequencies of both its center and surround mechanisms (and hence estimates of the center and surround widths or diameters) as well as of the responsivities of both the center and the surround at zero spatial frequency. Given these four parameters (two spatial dimensions and two responsivities at zero space frequency) we can use our difference-of-Gaussians "model," to predict the responsivity of the cell to other spatial patterns (at least to other patterns whose contrast is sinusoidally reversing at the same temporal frequency).

As an example we can predict how a cell might respond to an edge, ie, to a bipartite field undergoing sinusoidal contrast reversal. This is shown in Figure 11. The full curve is the predicted response to such a stimulus as a function of the distance of the bipartite field boundary from the midpoint of the receptive field. As usual the little pictures at the top attempt to show the spatial relationship of the stimulus pattern to the cell's receptive field for several different values of the spatial position. While the full line shows the response predicted from measurements previously made (on the same ganglion cell) with sine-wave gratings, the points represent measurements of the cell's response to an actual bipartite field stimulus. I think this gives a fair idea of the agreement that can normally be obtained between predictions based on spatial frequency responsivity measurements and experimental determinations of the responses to other stimulus patterns.

X-, Y- and Q-cells

Those of you who do not already know it will anyhow probably have guessed by now that not all cells behave as simply as those we have been talking about so far. In fact if you are just a beginner at recording from neurons with microelectrodes (as I certainly was when Christina Enroth-Cugell and I first started looking at cat retinal ganglion cells in this way) and if you set about recording from axons in the optic tract rather than directly from ganglion cells (as we first did) you will probably find (as we did) that the majority of ganglion cells whose axon spikes can be recorded satisfactorily do *not* behave in the simple way you have seen in Figure 8. What you would find instead is that the most easily studied cells behave in a very definitely non-linear manner even at contrast levels that are so low that the responses of these cells are barely detectable at all.

One of the most obvious ways of seeing this (and the one which first convinced Christina and myself that the population of retinal ganglion cells contained at least two different kinds of cell) is by looking at the responses which ganglion cells give when the screen at which the cat is looking is alternately switched from being uniformly illuminated to having on it a grating pattern of the same average luminance (Fig. 12). For a few of the cells from whose axons we first recorded

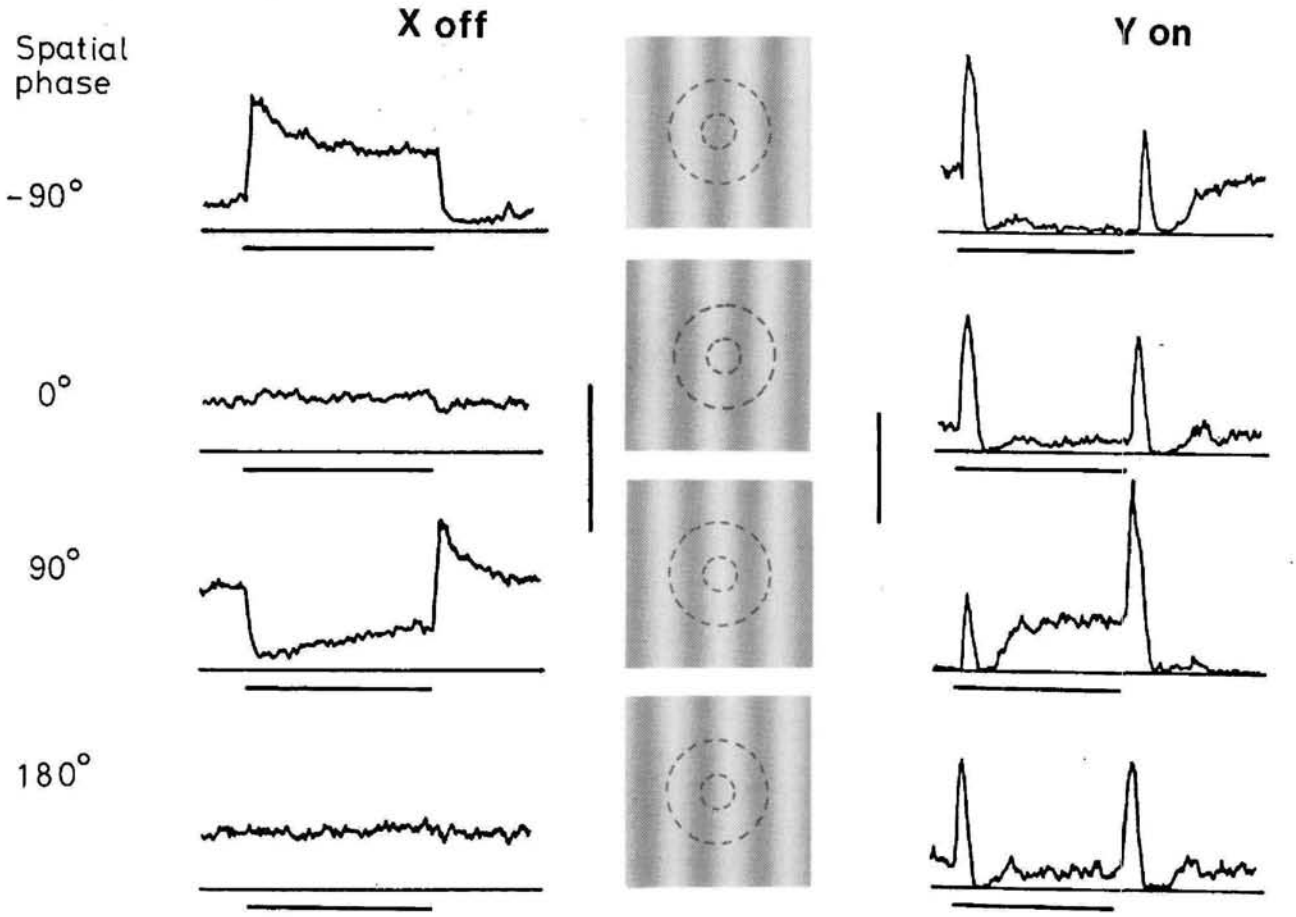

Fig. 12. Firing-rate records from a cat retinal OFF-center X-cell (left) and an ON-center Y-cell (right) responding to the appearance and disappearance of a sine-wave grating in different positions. The pictures in the middle show the positions of the stimulus pattern in relation to the receptive field during the period in which the pattern was present (1.1 seconds of every 2.2 seconds as marked by the bar under each record). When the pattern disappeared the stimulus screen remained at the same mean luminance. Note that the Y-cell generates a transient excitatory response at both appearance and disappearance of the stimulus pattern whatever its position (adapted from Enroth-Cugell & Robson, 1966). The vertical scale bar corresponds to a firing rate of 100 impulses/sec.

with some difficulty, the response to this stimulus was very dependent upon the spatial phase of the pattern (see left-hand set of records in Fig. 12). There clearly were positions, as I have already described for contrast-reversing patterns, at which there was essentially no response at all. These are the positions labelled 0 and 180 degrees and you can see the disappearance of the response of this OFF-center cell at these spatial phases. To cells which behaved in this way, that is to cells which in this way demonstrated linearity of spatial summation, we gave the non-descriptive name "X-cells." These same cells were subsequently called "brisk sustained" cells by Cleland & Levick (1974a) who identified them as a distinct class on the basis of other characteristics.

In contrast with the X-cells, the cells from whose axons we got the best recordings (presumably because they were large) behaved very differently as exemplified by the set of firing-rate records on the right in Figure 12. These cells, which again for no good reason (except that Y comes after X) we called Y-cells, gave responses which not only contained a component which changed with spatial phase in the same way as the responses of X-cells, but also an often much more visible transient burst of spikes both when the pattern was introduced as well as when it was turned off and the screen reverted to being uniformly illuminated. Indeed the capacity of cells of this type to respond transiently at very high firing rates fully justifies the name "brisk-transient cells" given to them by Cleland & Levick (1974a). The transient excitatory response which occurs more or less whenever there is some change in the stimulus and which persists even if the contrast of the stimulus is reduced to a very low level, indicates the existence of a strong non-linearity in the behavior of Y-cells. Moreover the existence of this response at all spatial phases of the stimulus and the non-existence of any position at which the response disappears altogether, serve to differentiate these cells from those cells showing linear behavior.

Figure 13 shows evidence of the same kind of non-linear behavior in the response of a Y-cell to contrast-

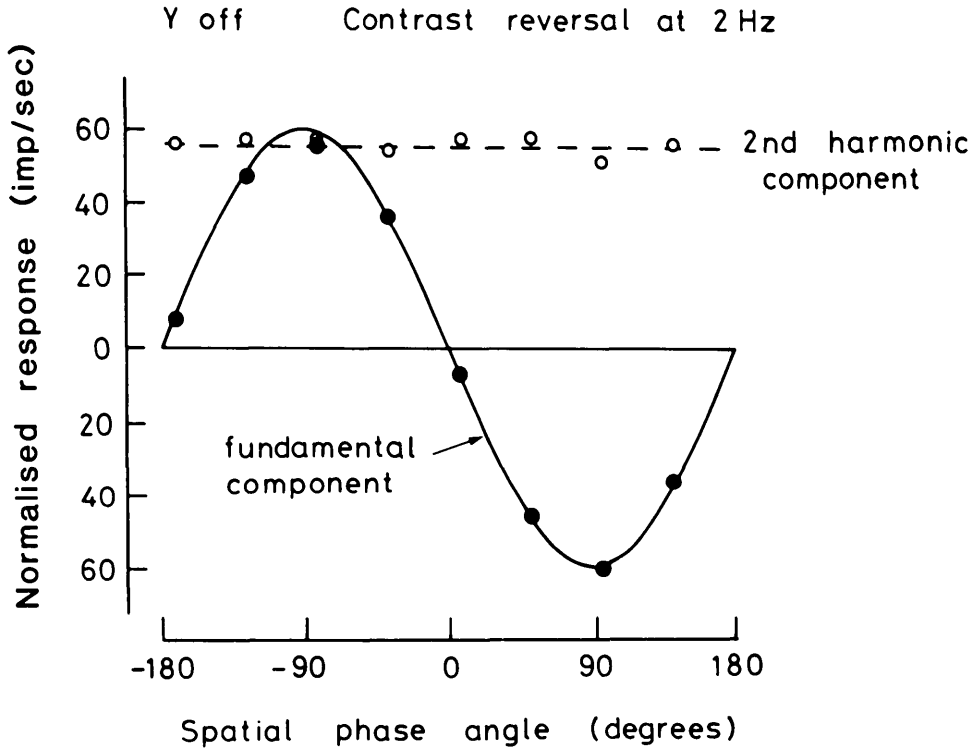

Fig. 13. Cat retinal OFF-center Y-cell. The filled symbols represent the amplitude of the fundamental component of the cell's response to a sinusoidally contrast-reversing grating as a function of the spatial phase of the stimulus. Compare this figure with Figure 8 which shows similar results for an X-cell. Note that the amplitude of the fundamental component of the response is a sinusoidal function of spatial phase and that at this spatial frequency (rather above the optimum for this cell) there is a large second harmonic response (open symbols) whose amplitude does not depend upon the position of the grating.

reversing sinusoidal gratings. The amplitude of the fundamental component (filled symbols and full line) of the response of this Y-cell to a sine-wave grating of relatively high spatial frequency depends upon the spatial phase of the pattern. As we saw for the X-cell in Figure 8, the amplitude of the fundamental component of the response of the Y-cell shown in Figure 13 also varies sinusoidally with the spatial phase of the grating. On the other hand, unlike the X-cell, the Y-cell shows a second harmonic component in its response (open symbols and broken line) which is not only about as large as the maximum value of the fundamental response, but is of constant amplitude independent of the position of the grating. A finding of this kind again demonstrates the existence of a strong non-linearity in the behavior of Y-cells and has been suggested by Hochstein & Shapley (1976), who have studied this aspect of ganglion-cell behavior in some detail, as a good way of identifying Y-cells.

Even though the Y-cell behaves so non-linearly that one cannot expect to model its spatial characteristics in the same simple way that is possible with X-cells, we can still usefully measure a spatial frequency responsivity function for these cells by looking simply at the amplitude of the fundamental component of their response to contrast-reversing gratings. When we do this we find that Y-cells have spatial frequency responsivity functions not unlike those of X-cells though there are two differences. In Figure 14 we have plotted the spatial frequency responsivity functions of three different retinal ganglion cells that were all close together on the retina so that we can properly compare them directly without worrying about the effect of the variation in properties of neurons in different retinal regions (eg, Peichl & Wässle, 1979; Cleland, Harding & Tulunay-Keesey, 1979). One obvious difference between the curves for the X and Y-cells is that the Y-cell curve is shifted to the left, that is to spatial frequencies which are about 3 times lower than for the X-cell curve. The Y-cell curve is also shifted upward with respect to the X-cell curve so that the peak responsivity of the Y-cell is about twice that of the X-cell. This is quite typical of the relationship we always find between the characteristics of X and Y cells in any one retinal region. The shift to the left of the descending high spatial frequency limb of the Y-cell curve indicates that the center of the Y-cell's receptive field has about three times the diameter of the equivalent X-cell receptive field center.

There is a third curve labelled Q in Figure 14. This is an example of the spatial frequency responsivity function of a third kind of cat retinal ganglion cell which Christina and I (in collaboration with Dan Schweitzer-Tong and Andrew Watson) have now studied using the same techniques as for X and Y cells (Enroth-Cugell, Robson, Schweitzer-Tong & Watson, 1983). The Q-cell type, a type which almost certainly corresponds to Stone & Fukada's (1974) tonic W-cell, or using Cleland & Levick's (1974b) terminology, to their "sluggish sustained" cell, is clearly different from both X and Y cells. However, Q-cells share some of their characteristics with Y-cells and some with X-

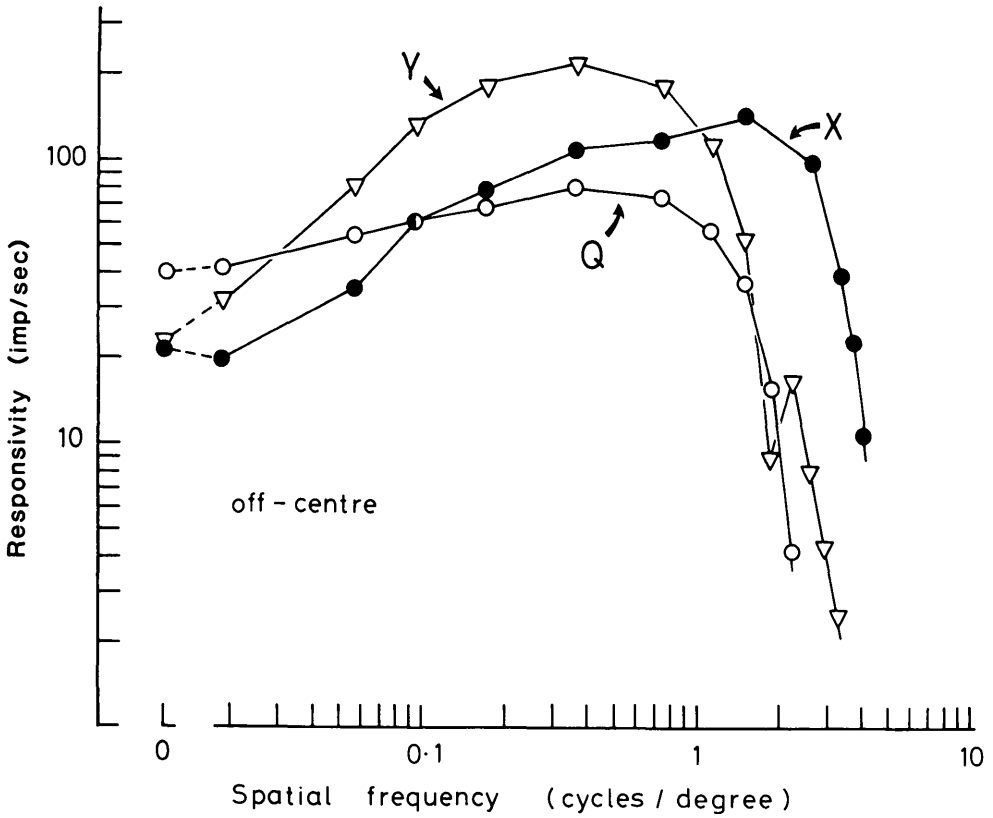

Fig. 14. Spatial-frequency responsivity functions for a trio of cat retinal OFF-center X-, Y-, and Q-cells encountered close together in the retina. Measurements made at 2 Hz.

cells. With an adjacent Y-cell a Q-cell has in common the size of its receptive-field center, ie, the spatial frequency responsivity functions of both Q and Y cells fall off at about the same high spatial frequency. On the other hand Q-cells share with X-cells the latters' characteristic linearity of behavior and in this respect they are quite unlike Y-cells. Moreover, as you can see from Figure 14, while a Q-cell may have its spatial frequency responsivity function in the same spatial frequency region as a neighboring Y-cell, its maximum responsivity is even lower than that of neighboring X-cells.

In Table 1, I have summarized these relations between the characteristics of neighboring X, Y, and Q-cells and added a couple more that do not come directly from looking at responses to gratings. A particularly interesting difference between X, Y, and Q-cells is in the regularity of their discharge. The regularity of the ongoing discharge of a Q-cell is typically much greater than that of an X-cell while the discharge of a Y-cell is typically somewhat less regular than that of an X-cell. The regularity of the discharge of Q-cells is usually so marked that one can be pretty certain that one is recording from a Q-cell as soon as its discharge is heard over the monitor loudspeaker. This is an extremely useful feature of Q-cell behavior for classifying these cells though its functional significance is not really very clear. It is worth noting, however, (as Derrington and Lennie, 1982, have pointed out) that we should probably take any difference in the variability of their discharges into account when we compare the sensitivities of different cells. Thus, although a given stimulus may produce a smaller response from a Q-cell than from a neighboring X or Y-cell, this smaller response of the Q-cell may be as detectable as the larger response of the noisier X or even Y-cell.

Table 1. Y- and Q-cells compared with X-cells

Cell type	X	Y	Q
Morphology	β	α	δ
Spatial summation	Linear	Non-linear	Linear
Relative center size	1	2.5–3.5	2–3
Relative retinal density	1	~1/10	~1/6
Temporal frequency response		Similar to X	Similar to X
Regularity of discharge		Less regular than X	More regular than X
Sensitivity (peak)		More sensitive than X	Less sensitive than X
Axonal conduction velocity		Faster than X	Slower than X

Another characteristic difference between X, Y and Q-cells which may be useful for purposes of identification (but which probably has no functional significance) is the difference in their conduction latencies, that is, in the time interval between electrically stimulating a ganglion cell's axon some distance downstream and recording an action potential near its soma. This latency difference stems from the different conduction velocities of the axons of the different cell types and presumably reflects differences in axonal diameter (Cleland, Dubin & Levick, 1971). It was probably the first indication that we should expect to

find morphological differences between these three functionally-defined cell-types.

This brings me to my very last point and takes us back to the beginning of our story and the work of those skilled in histological techniques who now not only peer down microscopes but are also expert in applying the new methods available for showing up single neurons as well as the electrophysiological identification of the cells they look at. Thanks to such people it is now more or less certain which functional type corresponds to which morphological type. In this context we must largely be grateful to Heinz Wässle and his collaborators (eg, Cleland, Levick & Wässle, 1975; Wässle, Boycott & Illing, 1981) for identifying X and Y-cells with the beta- and alpha-cells which Boycott & Wässle (1974) had previously described in the cat retina while more recently, Saito (1983) has shown in a beautiful set of experiments that the regularly firing cells of the cat retina, presumably Q-cells, are morphologically Boycott & Wässle's delta-cells. Of course there are several more types of functionally distinct ganglion cell with even smaller axons which have been described by others (eg, see the review by Rodieck, 1979) but these have not yet been fully characterised, and it remains to be seen whether spatial frequency methods of doing this can be usefully applied to them.

Well, that is the end of the science but before I step down just a few words of thanks. First, of course, my thanks to Mat Alpern for his very kind (not to say unduly flattering) introduction. Mat is a very dear friend of long standing (one of the many good friends I have in fact made through my work in vision) and I hope he won't mind if I say that some of his remarks should perhaps be taken with a pinch of salt. Anyway thank you Mat.

Secondly, I must thank Christina herself. But I owe Christina so much for what she has done for me (or should that be *to* me?) that I can't adequately thank her in a few words. Let me just say here that without her this work would never have been started, wouldn't have been continued, wouldn't have been developed, wouldn't have been finished—certainly wouldn't have been written up. Thank you, Christina, for everything.

Finally, thank *you*. You, the audience, for listening to us so patiently and you, as you embody the Association for Research in Vision and Ophthalmology, for bestowing upon us this award. Thank you ARVO.

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